ABSTRACT

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Stream ecosystems are profoundly degraded by watershed urbanization. Hydrologic, geomorphic, chemical and thermal adjustment following urban development contributes to substantial biodiversity loss in impacted streams. However, the extent of degradation along an urban gradient may not be uniform among regions. The hydrogeologic and climatic setting in which a stream is located may influence the severity of abiotic and biotic impact induced by urban development. I explored and compared differences in stream ecosystem responses to urbanization between the Coastal Plain and Piedmont physiographic regions of the eastern United States. Taxon-specific responses of fishes and macroinvertebrates as well as the coherence of benthic invertebrate communities along gradients of landscape stressors were quantified. Hydrologic, chemical and thermal impact induced by watershed urbanization was compared between the two physiographic provinces using existent large datasets collected by various governmental entities. I also compared the severity geomorphic and sediment regime alteration in urban streams between regions using direct measurements of channel morphometry and *in situ* natural experiments within selected watersheds. Biotic sensitivity to urbanization was consistently found to be

heightened in Piedmont streams relative to those in the Coastal Plain. Such trends were consistently observed for fish and macroinvertebrate taxa as well as for invertebrate community coherence. The most tolerant macroinvertebrate communities were associated with low channel slopes, effective soil permeability and high levels of wetland cover. Rural Coastal Plain streams exhibited fewer flood events that were longer in duration; however, flood hydrology was more impacted by urbanization in Coastal Plain streams relative to those of the Piedmont. Conversely, thermal impact induced by urbanization was greater in Piedmont streams. Experimental observations concluded that benthic sediment size structure, deposition and transport were more impacted by urban development in Piedmont streams relative to those of the Coastal Plain. My findings highlight interregional heterogeneity in stream ecosystem responses to landscape change, suggesting that effective watershed management decisions may need to consider the physiographic setting in order to improve efficacy. Furthermore, results suggest that watersheds characteristic of hydrogeomorphic attributes that effectively transfer water to channels during precipitation events may be acutely vulnerable to urban development.

INTERREGIONAL DIFFERENCES IN STREAM ECOSYSTEM RESPONSES TO URBANIZATION: CAUSES AND CONSEQUENCES

by

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Dedicated to Mom, of course

and

to Bob and Connie Utz, whose selfless, loving efforts helped me become a man capable of producing work such as this.

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CHAPTER I

INTRODUCTION

The conversion of land from natural cover for human-centered use ranks as the primary driver behind the modern extinction event among most biomes and ecosystems (Sala et al. 2000). Approximately 15 and 20% of global forest and grassland cover, respectively, has been converted for agricultural use (Sisk et al. 1994). In many eastern United States counties, the area covered by exurban land has grown >60% between 1950 and 2000 (Brown et al. 2005a). While such practices result in direct habitat loss, the relationship between land use change, ecosystem degradation and the corresponding impact on biota may be complex. Differential geoclimatic conditions among regions may render one area more prone to degradation and species loss to land cover change than others, even when species composition is similar (Huggett 2005). Loss of species in fragmented habitats may occur decades or centuries subsequent to patch isolation (Hilderbrand 2003, Lindborg and Ericksson 2004, Vellend et al. 2006); physicochemical responses to land cover change may evolve over such temporal scales as well (Jacobson and Coleman 1986). Further, invasions of non-native species and/or compositional shifts from sensitive to tolerant taxa in degraded habitats may buffer declines in measures of biodiversity, such as species richness (Walters et al. 2003).

Stream ecosystems are particularly vulnerable to landscape change (Sala et al. 2000, Allan 2004) as streams are tightly linked to watersheds (Hynes 1975). Urban and exurban development invoke dramatic physical and chemical changes in streams. Runoff from urban land may increase nutrient, metal, and fine sediment

concentrations (Lenat and Crawford 1994, Rogers et al. 2002, Chadwick et al. 2006, Cunningham et al. 2009). Stream temperature regimes often shift due to urbanization, including increasing summer and decreasing winter means and elevated year-round diurnal variability (Klein 1979, Arnold and Gibbons 1996, Paul and Meyer 2001). Impervious surfaces guide storm water either directly to the stream channel or to points that develop channels to streams. The consequences can include increased surface runoff during spates (Arnold and Gibbons 1996, Roy et al. 2005) and a corresponding shift in recurrence intervals for floods (Hollis 1975, Degasperi et al. 2009), an increase in bankfull discharge (Booth and Jackson 1997), reduced baseflows (Klein 1979, Rose and Peters 2001), and reduced recession periods and baseflow recession constants following spates (Konrad et al. 2005, Roy et al. 2005). Such change in hydrology affects channel morphology. Channel widening, bankfull depth incision, and bank instability typically ensue (Leopold 1973, Klein 1979, Booth 1990, Wang et al. 2001, Grable and Harden 2006). Changes in channel sediment regimes following urbanization typically evolve over time. Initially, construction activity produces a pulse of benthic fine sediments but eventually elevated flows reduce fine sediment concentrations (Wolman 1967, Pizzuto et al. 2000, Colosimo and Wilcock 2007, Schoonover et al. 2007).

Agricultural practices alter chemical and physical stream properties as well. In the United States Mid-Atlantic highlands, catchment percent agriculture accounted for 50% of the variation in total nitrate as nitrogen in streams (Jones et al. 2001). Such increases in nutrient levels in streams may promote excessive algal growth, which can decrease dissolved oxygen concentrations. Agriculture has been positively

correlated with increasing proportions of benthic and suspended fine sediment concentrations, as exposed soil erodes to channels during spates (Jordan et al. 1997a, Cuffney et al. 2000, Jones et al. 2001, Sutherland et al. 2002, Donohue et al. 2006). Temperature regimes may be affected in agricultural streams via removal of riparian vegetation that would otherwise shade channels (Wehrly et al. 2006). Disruptions to the hydrologic properties of agricultural streams may occur by reduction in infiltration capacity and the delivery of strong pulses of water during events (Poff et al. 1997), though urban land use may substantially exceed agricultural in terms of altering stream hydrologic properties (Allan 2004, Poff et al. 2006).

As the consequences of land use change on stream ecosystems have long been recognized, studies exploring how such practices affect lotic biota have flourished with advances in spatial analysis. The most common work relates an index of biotic integrity (IBI), similar metrics, or multivariate community-based measures to land cover change, typically the percentage within catchments. Using such techniques, a growing wealth of studies have demonstrated biotic change along urban (Klein 1979, Lenat and Crawford 1994, Hall et al. 1996, Wang et al. 1997, Walsh et al. 2001, Wang et al. 2001, Rogers et al. 2002, Roy et al. 2003, King et al. 2005, Moore and Palmer 2005, Moerke et al. 2004, Meador et al. 2005, Stanfield and Kilgour 2006, Megan et al. 2007, Goetz and Fiske 2008, Smith and Lamp 2008, Degasperi et al. 2009) and agricultural (DeLong and Brusven 1998, Lammert and Allan 1999, Cuffney et al. 2000, Sponseller et al. 2001, Harding et al. 2003, Melo et al. 2003, Donohue et al. 2006, Baker et al. 2007) gradients.

Despite this extensive body of work demonstrating how land use affects streams, many issues demand additional attention to effectively conserve lotic resources in the face of future land development. A critical (yet typically neglected) dynamic involves potential differences in ecosystem sensitivity to land use change among stream forms. Streams naturally vary in form and function among differing geoclimatic settings (Poff and Ward 1989, Rosgen 1996). Considering such inherent form diversity, rates of physicochemical and biological degradation per unit land use change likely vary among regions. Yet most studies mentioned above quantify degradation within one geoclimatic region; exceptions typically explore changes in IBI or multimetric responses without consideration of regional dynamics. When biotic responses to land use change among physiographic regions are recognized, they are often attributed to patterns in land use intensity (Kennen et al. 1999) and possible region-specific sensitivity is not addressed. Further, using a single IBI among regions may be inappropriate, as regions often possess different characteristic biota. The potential for region-specific rates of degradation and consequences for landscape-scale conservation prompted several authors (Karr and Chu 1999, 2000, Allan 2004) to call for research that explicitly examines the role of geoclimatic variation in stream ecosystem responses to land use change.

A handful of efforts have answered this call by examining how streams respond to land use change among geoclimatic regions. Poff et al. (2006) explores changes in hydrologic regimes along agricultural and urban watershed gradients among four large-scale regions of the United States. Variation in geoclimatic conditions among regions resulted in different response patterns. For instance, agriculture caused an

increase in flow duration in all streams (northwest, midwest, southwest) except those in the southeast, where flow duration was reduced. Sprague and Nowell (2008) demonstrated highly variable concentrations of specific herbicides and pesticides in urban streams among six metropolitan areas of the United States. Several studies organized by the United States Geological Survey's National Water Quality Assessment (NAWQA) program compared biotic, chemical and physical responses of streams along urban gradients in the Birmingham, Boston, and Salt Lake City metropolitan regions (Brown et al. 2005b). Responses of variables in urbanized streams varied considerably. Fish species richness declined more in Birmingham urban streams relative to those in Boston (Meador et al. 2005). Macroinvertebrate density increased only in Boston area urban streams due to elevated hydropsychid caddisfly densities, elsewhere, overall density declined (Cuffney et al. 2005). Elevated fine sediment concentrations were observed in urban Boston and Salt Lake City streams, but not in Birmingham. Curiously, some variables changed similarly or not at all in urbanized streams of the three cities: many multivariate and multimetric macroinvertebrate response variables responded with similar slopes (Cuffney et al. 2005), and a number of habitat metrics (e.g., width and sinuosity) changed little along urban gradients in all three regions (Short et al. 2005).

The above efforts demonstrate the importance of identifying regional differences when assessing stream responses to land use change. Clearly, management actions meant to retain lotic resources in changing watersheds must carefully acknowledge region-specific responses in order to be effective. Yet the work discussed above addresses the issue of differing response patterns in streams that vary dramatically in

geoclimatic settings (ranging from arid to humid climates and spanning a broad array of geologic and topographic features) and characteristic biota. Differential sensitivity may also occur among regions at smaller spatial scales, as spatially adjacent physiographic regions vary in geoclimatic features as well (Thornbury 1965, Omernik 1987). Quantifying differential stream responses to land use change at smaller scales will improve the effectiveness of conservation efforts, which are liable to develop within smaller political boundaries than the contiguous United States. Further, sensitivity differences may occur within physiographic regions as well. For instance, streams in watersheds draining specific geologic classes and/or below a certain basin size may be acutely sensitive to land use change relative to others in the same region.

The lack of studies quantifying taxon-specific responses to land use change is another shortcoming of traditional land use-stream degradation studies. Streams possess exceptional biodiversity (Master et al. 2001, Abell 2002, Strayer 2006) including a disproportionate number of threatened and endangered species (Master et al. 2001, USFWS 2008). The multimetric and multivariate nature of most studies quantifying land use driven stream degradation offers little insight regarding responses of individual taxa. The most common sensitivity information available for specific taxa is tolerance values used for developing biotic indices (Hilsenhoff 1987, Lenat 1993, Barbour et al. 1999, Yuan 2004, Cuffney et al. 2005, Bressler et al. 2006, Blinn and Ruiter 2006). These unitless values most often quantify sensitivity to stressors in general. When they do convey sensitivity to a specific stressor, deriving meaning for management decisions may be difficult. For instance, determining the maximum level of a particular stressor a taxon is capable of enduring, or interpreting

how an organism responds, can be difficult or impossible using tolerance values. Yet addressing such questions may be critical to inform management decisions involving threatened species or for modeling future loss of biodiversity (Nilsson et al. 2003) as well as for developing more precise ecological indicators. Finally, quantifying taxon-specific responses to land use may enhance understanding of region-specific ecosystem sensitivity, as the responses of taxa found between regions may be compared. Not only could region-specific differences generate new hypotheses and understanding, but the results would better guide management and planning to minimize biodiversity loss as land uses change with the expanding human population.

Addressing the problems discussed above will increase the success of landscape-scale stream conservation management decisions and improve our general understanding of how streams respond to land uses. My proposed research will use a large stream ecosystem and geographic information database as well as several *in situ* natural experiments to explore differential sensitivity to land uses in streams among distinct geoclimatic regions. The database will also be used to catalogue taxa responses to land use change for fishes and invertebrates among regions. My dissertation includes five chapters that address the following objectives:

Objective 1-Quantify, catalogue, and summarize fish and macroinvertebrate taxon-specific responses to landscape change among multiple regions.

Objective 2-Quantify and compare vulnerability to urbanization among Coastal Plain and Piedmont macroinvertebrate communities and determine potential factors driving observed differences in sensitivity.

Objective 3-Quantify differences in geomorphic and physicochemical responses to urbanization between Coastal Plain and Piedmont streams.

The following dissertation overview includes questions posited to address the stated objectives:

Q_1-How do taxon-specific responses to land use change vary specifically and broadly among geoclimatic regions?

Q_2-Are taxa with greatest conservation need (GCN) status susceptible to land use change and are there taxa without GCN status that are acutely vulnerable?

Q_3-Are traditional indicator organisms or other taxa the most appropriate to detect the effects of land use?

As discussed above, streams possess high biodiversity that include threatened species in need of conservation efforts. Susceptibility to land use change could vary by region at the species scale (or higher taxonomic unit) scale. I will use the Maryland Biological Stream Survey (MBSS) database to catalog fish and macroinvertebrate responses to land cover classes that address Objective 1 through the above questions. Rather than calculate traditional unitless tolerance values for each taxon, however, I will quantify sensitivity using a novel approach that detects if an organism responds positively, negatively, or neutrally to land use. For sensitive organisms, unit-specific estimates of the maximum degree of watershed development tolerated and the degree that may initiate an impact will be provided for each taxon. These findings will further our understanding of differential responses to land use by region, assist in species-specific management decisions for threatened taxa, and help

interpret the patterns observed when traditional multivariate metrics change along land cover gradients.

Q_4-How does invertebrate community sensitivity to land use vary broadly between Piedmont and Coastal Plain physiographic regions?

Q_5-Do parameters associated with Coastal Plain watersheds and ability to retain water on the landscape (i.e. low topographic relief; deep, permeable soils) confer community resilience to urbanization?

In addressing Objective 2, questions four and five depart from previous research by not simply addressing whether or not communities are affected by land use change, but by exploring how community degradation rates vary among regions and watersheds with specific attributes. Preliminary evidence and two related studies (Morgan and Cushman 2005, Baker et al. 2007) suggest that biotic responses to urban and agricultural land use differ between the Piedmont and Coastal Plain physiographic provinces. Yet the above studies compared dissimilar (thus not directly comparable) response variables: IBI's constructed using different metrics and organisms for each region. I will address the above questions with MBSS data using techniques similar to those used to identify communities associated with environmental variables in streams elsewhere (Hawkins et al. 2000, Stoddard 2004, Heino 2005) but take the effort further by quantifying the sensitivity of each community to land use change separately. Therefore this dissertation component will identify acutely sensitive and relatively tolerant communities (along with their associated stream forms) in addition to determining if community-scale vulnerability to urbanization varies by physiographic region as observed at the taxon-specific scale.

Further, the severity of impact in streams is often associated with the amount of water delivered from impervious surfaces during spates (Booth 2005, Roy et al. 2005), and several parameters associated with the Coastal Plain (i.e. deep, permeable soils and low topographic relief) suggest that water retention may be higher in that province. I will therefore test these variables as drivers of resilience to change from urbanization. In other words, are watersheds with high water retention ability consistently (i.e., both within and among regions) less sensitive to increasing urbanization?

Q_6-How do rates of macroinvertebrate habitat recolonization following physical disturbance vary between rural and urbanized streams in the Piedmont and Coastal Plain?

The severity and frequency of flow-driven disturbance is a major driver of community structure in streams (McAuliffe 1984, Poff and Ward 1989, Mackay 1992, Robinson et al. 1993, Death and Winterbourn 1994, Townsend et al. 1997, Knight et al. 2008), as even moderate flows may displace, redistribute, and/or cause injury or death to lotic organisms (Matthaei et al. 1997, Gibbins et al. 2007a). Thus the increased frequency of flood flows (especially low to moderate intensity) may be a primary mechanism causing biodiversity loss in urban streams. Yet natural (and thus potentially urban) flow regimens between Piedmont and Coastal Plain streams are inherently different (Moglen et al. 2006). Further, geomorphic features such as sediment structure, sinuosity and characteristic habitat may interactively affect how spates impact benthic organisms; these features also vary between regions. Benthic organisms in one province may be naturally more adapted to urban-type flow regimes than another. One means of quantifying how communities cope with physical

disturbance is to observe how rapidly patches of habitat are recolonized following an event that displaces organisms, which will partially address Objective 2. Rates of recolonization in disturbed and newly available benthic habitat in urban and rural streams of the two provinces will be compared in the same sites chosen for the comparative urban geomorphology component.

Q_7-How does the severity of physicochemical change induced by urbanization differ between streams in the Coastal Plain and Piedmont physiographic provinces?

Preliminary analyses pertaining to Objective 1 provide a partial answer to questions Q_1 and Q_4: biota in Coastal Plain streams appear to be less sensitive to urbanization relative to those of the Piedmont. Land use, however, represents a dependent surrogate variable for multiple physicochemical stressors that extirpate lotic organisms. If dichotomous sensitivity to land use is observed between regions, differences in physical, chemical, and geomorphic responses to urbanization likely also occur. A wealth of data on mid-Atlantic streams are available to answer question Q_7 posited above. Rather than deriving models meant to predict nutrient export or hydrologic regimen details, this dissertation component will test whether or not the characteristic shifts in stream physiochemical properties caused by urbanization are more severe in Piedmont streams. Such tests will be conducted on multiple parameters, including many collected by the MBSS program (chemical and temperature datasets) as well as stream flow characteristics derived from USGS stream gauge data. The diversity of physicochemical changes to be explored

(combined with the geomorphic experiments detailed below) may highlight potential the mechanisms driving differences in biotic sensitivity between the two provinces.

Q_8-How does the severity of geomorphic responses to urbanization differ between streams in the Coastal Plain and Piedmont physiographic provinces?

Geomorphic stream properties also change due to watershed urbanization, yet characteristic responses may vary substantially among regions. Differences in geomorphic adjustment in urban streams among regions could partially drive the patterns observed in biotic sensitivity to urbanization between Coastal Plain and Piedmont streams. Question 8 will be answered using a suite of *in situ* experiments and field measurements in small rural and urbanized streams of both ecoregions. Bed stability, sediment transport, water quality during spates, and channel morphology will be assessed to test for differences in urbanization-induced change between regions. These analyses will compliment the examination of physicochemical differences between regions to produce a comprehensive depiction of region-specific abiotic change in urban impacted streams.

My dissertation will therefore comprehensively quantify regional differences in stream responses to land use change, particularly urbanization, as called for by Allan (2004) and Karr and Chu (1999, 2001). The work will depart from similar efforts (such as the NAWQA comparative study) in that trends are identified in contiguous regions, where characteristic biota are partially shared among regions and landscape-scale conservation measures are more likely to develop. Additionally, the methodology used to characterize biotic sensitivity will identify acutely vulnerable specific taxa, communities, and the landscape factors that drive such differences in

sensitivity. The regional assessment of physicochemical and geomorphic response patterns will elucidate potential abiotic mechanisms driving the trends observed in biotic responses. Findings from my study will also inform landscape-scale conservation measures throughout much of the eastern United States (as the Coastal Plain and Piedmont physiographic provinces range from New Jersey to Alabama). Further, my research may provide a framework to predict differences in land use driven stream degradation in regions geoclimatically similar to the Coastal Plain and Piedmont and highlight the importance of considering physiography when establishing land use-stream ecosystem relationships elsewhere.

CHAPTER II

TAXON-SPECIFIC RESPONSES OF BENTHIC MACROINVERTEBRATES TO LAND COVER CHANGE

(At the time of dissertation submission, this chapter has been published in volume 9 of the journal Ecological Indicators, titled "Identifying regional differences in threshold responses of aquatic invertebrates to land cover gradients" by R.M. Utz, R.H. Hilderbrand, and D.M. Boward; pages 556-567.)

Indicator taxa can be viewed as ecological threshold detectors. Each taxon may exhibit a unique response to a particular stressor (Gibbs 1998, Fahrig 2001), and we can use their different sensitivities to assess how far a system has departed from its base state. Such information can also be used to forecast biodiversity loss as conditions change along a disturbance gradient. In addition to the modern idea of ecological thresholds where a rapid nonlinear response occurs (e.g. Huggett 2005, Groffman et al. 2006), at least two additional ecological thresholds are important for monitoring and assessment: lower and upper response limits. The lower response limit represents the stressor value at which a negative effect initiates. We believe this to be important because a response can negatively affect a population long before it enters into the phase of rapid nonlinear change, particularly for those systems that respond linearly. Identifying the initiation of impact can be quite important to planning, management, and conservation. Similarly, the upper limit threshold is valuable as it signals the point along a disturbance gradient where an indicator essentially disappears from the landscape.

Stream-dwelling benthic macroinvertebrates are commonly used for indicator purposes (see Rosenberg et al. 2008 for a thorough review) and represent a group of

organisms that are increasingly under threat (Strayer 2006). Benthic macroinvertebrates are ubiquitous in aquatic habitats (Vinson and Hawkins 1998), widely diverse in both species richness (Allan and Castillo 2007) and sensitivity to pollution (Barbour et al. 1999), and are easily collected in the field. Despite the widespread use of these organisms as indicators, however, the information regarding sensitivities of specific taxa to particular stressors is limited in scope. The most readily available macroinvertebrate sensitivity information are unitless tolerance values meant to estimate relative sensitivity either to targeted stressors such as organic pollution or sedimentation (Hilsenhoff 1987, Lenat 1993, Blinn and Ruiter 2006) or to multiple disparate stressors (Barbour et al. 1999, Yuan 2004, Bessler et al. 2006). Such tolerance values are useful for constructing and applying many community based systems for biomonitoring use. However, basic ecological questions concerning a taxon may be difficult to answer with tolerance values alone. For instance: at what level of a particular stressor do organisms disappear? Which organisms respond to a potential stressor negatively, positively, or not at all? Are there additional taxa that may be good candidates for detecting degradation?

Conversion of land cover from forest to human-altered forms is a major driver in the degradation of stream ecosystems (Abell 2001, Strayer 2006). Urban-associated cover induces substantial change in multiple physicochemical properties of streams (reviewed by Paul and Meyer 2001 and Walsh et al. 2005) and local loss of biodiversity. Agricultural land use also affects stream form and function, often with consequential loss of biota (Cuffney et al. 2000, Jones et al. 2001, Sutherland et al.

2002, Donohue et al. 2006), though the effects from urbanization appear to be more severe (Allan 2004, Poff et al. 2006).

Because streams differ substantially in form and function with variations in topography, geology, and climactic characteristics (Poff and Ward 1989, Rosgen 1996), the effects of land cover on aquatic organisms may differ among regions. Regional differences may also occur in responses of benthos (Stanfield and Kilgour 2006), but not be detected with many methods (Cuffney et al. 2005) or assessment methods are adjusted so that indices respond similarly to stressors among regions (Astin 2006, Southerland et al. 2007). A more thorough examination using individual taxa is warranted because response differences among regions could have large implications for ecological assessments and their applications.

Here, we present a method to assess taxa responses along a stressor gradient. Specifically, we analyze benthic macroinvertebrate taxa collected in different regions and their responses to land cover, but the method is sufficiently flexible to assess a wide range of organisms to numerous stressors. Our objectives are to 1) introduce a robust technique that describes the response distribution of a taxon along a stressor gradient; 2) catalogue macroinvertebrate responses as supplemental material to aid future assessment approaches and for baseline response information for conservation and management; and 3) assess the influence of spatial scale on ecological thresholds.

Methods

Study area

The state of Maryland encompasses about 32,000 km^2 of land in the mid-Atlantic United States. Nearly all watersheds in the state drain into the Chesapeake Bay, with

a small area (~1,100 km^2) draining into the Ohio River watershed in far western Maryland, and some emptying directly into the Atlantic Ocean in southeastern Maryland (430 km^2). Three broad regions fall within the state: the Coastal Plain, Eastern Piedmont (both true physiographic provinces) and the Highlands (a conglomerate of the Appalachian Plateau, Ridge and Valley, and Blue Ridge physiographic provinces, Fig. 1). The Coastal Plain comprises land below the fall line in eastern Maryland and consists of land adjacent to the Chesapeake Bay. The Piedmont province is located above the fall line and west to the Blue Ridge Mountains.

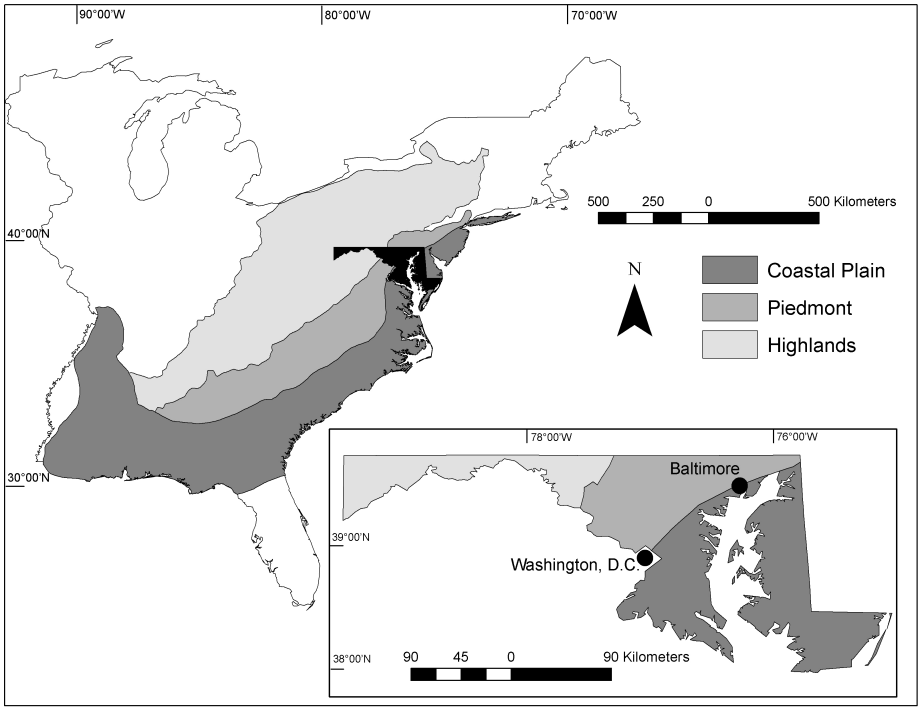

Figure 1. Map of the eastern United States and the state of Maryland illustrating the physiographic regions delineated for taxon-specific analysis

Each region possesses differing physical and ecological attributes. Cluster analyses of both fish and invertebrate data have shown that these regions are

ecologically distinguishable (Stribling et al. 1998, Roth et al. 2000, Killian 2004, Southerland 2007). Some benthic invertebrate genera are only found either above or below the fall line (i.e. Coastal Plain versus Piedmont and Highlands) or exclusively in one region. Differences in ecological characteristics between regions may be partly explained by the physical attributes of each zone. Coastal Plain streams are characterized by low gradient, high sinuosity, and small substrate particle sizes such as silt and sand (King et al. 2005, Barker et al. 2006) while most streams in the Highlands feature the opposite characteristics (high gradient, low sinuosity, and larger substrate particle sizes such as cobble and boulders). Piedmont streams typically represent intermediate physical conditions between the Coastal Plain and Highlands provinces, although many feature steep gradients and a larger sediment particle size composition as in the Highlands.

Biological data

Macroinvertebrate data were extracted from rounds one (1995-1997) and two (2000-2004) of the Maryland Biological Stream Survey dataset (MBSS, Klauda et al. 1998). The MBSS uses a probability-based design for site selection in order to maximize representation of conditions statewide. The 75m-reach sites are randomly selected for sampling and stratified within a subset of major river basins each year. As a result, each 75m stream reach within the state has a non-zero probability of being selected for sampling over a three year interval.

Macroinvertebrates were collected at all MBSS sites during spring baseflow (March and April), when the likelihood of collecting all representative taxa is greatest. Sites were limited to wadable streams; most were first- through third-

Strahler order with a small number (n=36) exceeding third-order. Within each 75 m reach, 1.86 m^2 (20 ft^2) of site-specific characteristic habitat were sampled using a D-net (Kazyak 2001). Substrate upstream of the D-net was disturbed by kicking and moving by hand, and organic debris such as wood and leaves was rubbed by hand or a small brush. Large organic matter collected in the net was inspected for organisms and then removed. Samples were preserved in a 70% ethanol solution. The collected benthic organisms were subsampled and identified to genus or lowest practical taxon, with the exception of Oligochaeta (to family level). All organisms were identified using stereoscopes except Chironomidae and Oligochaeta, which were slide-mounted and identified using a compound microscope. Further detail on taxonomic identification procedures and quality control may be found in Boward and Friedman (2000). Data for the current study were derived from 2,303 invertebrate samples from 1,953 stream reaches (350 sites were sampled more than once). Of these sites, 873 were collected in the Coastal Plain, 862 in the Piedmont, and 568 in the Highlands region.

Land cover data

Catchment land cover was calculated for all MBSS sites. Watershed boundaries were determined using the 30 m resolution national digital elevation dataset (U.S. Geological Survey). The land cover layer was provided by the National Land Cover Database (NLCD), a 30 m resolution raster data set taken via thematic imaging during 2001 (USEPA 2008). Land covers within each watershed were extracted from the NLCD in a GIS.

To simplify analyses of catchment land cover, land cover designation was limited to Class-I categories (see USEPA 2008 for a full description of all classes described below). Urban land represented low, medium, and high intensity developed land along with open space urban development. Agricultural land cover represented the sum of the pasture/hay and cultivated crop categories. The area of each summed category (urban and agricultural land cover) was divided by the area of each watershed to estimate the percentage of developed and agricultural land. The NLCD dataset also includes an estimate of percent impervious surface cover (ISC- pavement, rooftops, and other surfaces that prohibit water permeation) from 0 to 100 on a $30m^2$ pixel scale; the total percent of impervious surface covering each watershed was calculated from this layer. Though urban cover is highly correlated with ISC (Pearson correlation coefficient=0.94, $p<0.0001$ in sampled sites), the latter is considered a more parsimonious land cover class to predict the impact of urban development on stream ecosystems (Arnold and Gibbons 1996). We therefore assessed sensitivity to both ISC and urbanization. The percentages of cover for each category were those used in testing for catchment land cover effects on invertebrate distributions.

The distribution of land cover classes in sampled streams among the three regions varied in some instances but was similar in others. Largely due to growth of the Baltimore and Washington, D.C. metropolitan areas (Fig. 1), urban land coverage is concentrated in the Coastal Plain and Piedmont regions of Maryland. Sites in these two provinces sampled by the MBSS program were very similarly distributed along an urbanization gradient (Fig. 2). Urban watersheds were rarely sampled in the Highlands due to an absence of metropolitan centers in this region (Fig. 2).

Agricultural cover was more uniformly distributed among regions, though Piedmont watersheds tended to possess more agricultural cover, and many Highlands watersheds were composed of natural cover (forests and wetlands; Fig. 2). Table 1 provides Pearson correlation coefficients of sample site land use classes by region. Although climate varies moderately throughout Maryland, agriculture is largely homogeneous among regions. In all three regions the dominant crops are soybeans and corn (MDA 2003). Agricultural productivity varies more among counties than among the three regions delineated for the current study (MDA 2003).

Data analysis

We compared the cumulative frequency distributions (CFD) of land cover between those sites where a taxon would be expected to occur and the actual group of sites in which a taxon did occur, allowing both rare and common taxa to be compared independent of the collection frequency. The process is described below and in Fig. 3. All genera tested for an effect from land cover required a minimum of twenty-five collection occurrences before being tested; genera collected <25 times within a region were considered too rare for analysis. Urban and impervious cover relationships were calculated for taxa in the Coastal Plain and Piedmont physiographic provinces, but not in the Highlands region, where the total amount and distribution of urban land was considered too sparse for analysis. Responses to agricultural land cover were examined for each region.

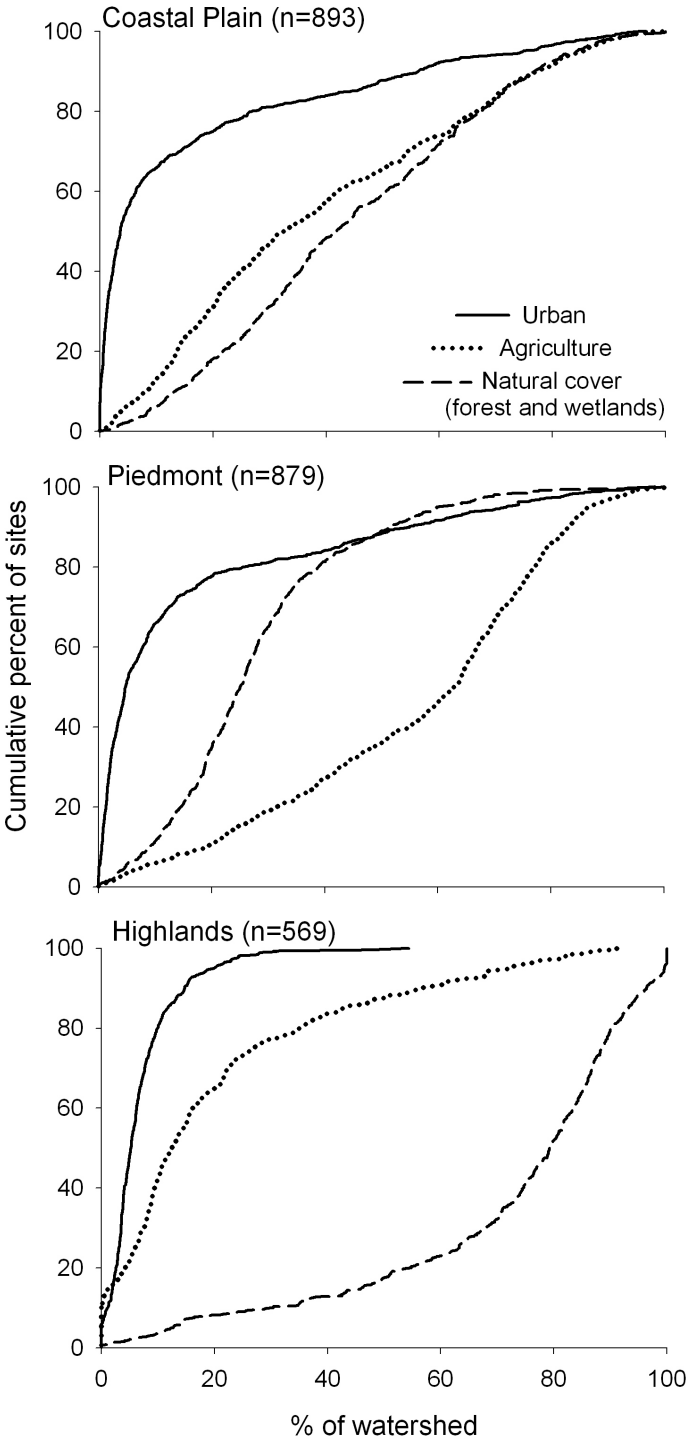

Figure 2. Cumulative distribution of watershed land use classes for sites sampled by the MBSS program delineated by region. The number of sites sampled per region is provided in the upper left corner.

Table 1. Pearson correlation coefficients of watershed land use classes among regions. Natural cover includes forests and wetlands; 'Ag' refers to agricultural cover. p-values for all correlations are <0.0001.

	Coastal Plain		Piedmont		Highlands	
	Urban	Ag	Urban	Ag	Urban	Ag
Ag	-0.542		-0.746		0.282	
Natural	-0.374	-0.551	-0.274	-0.435	-0.535	-0.959

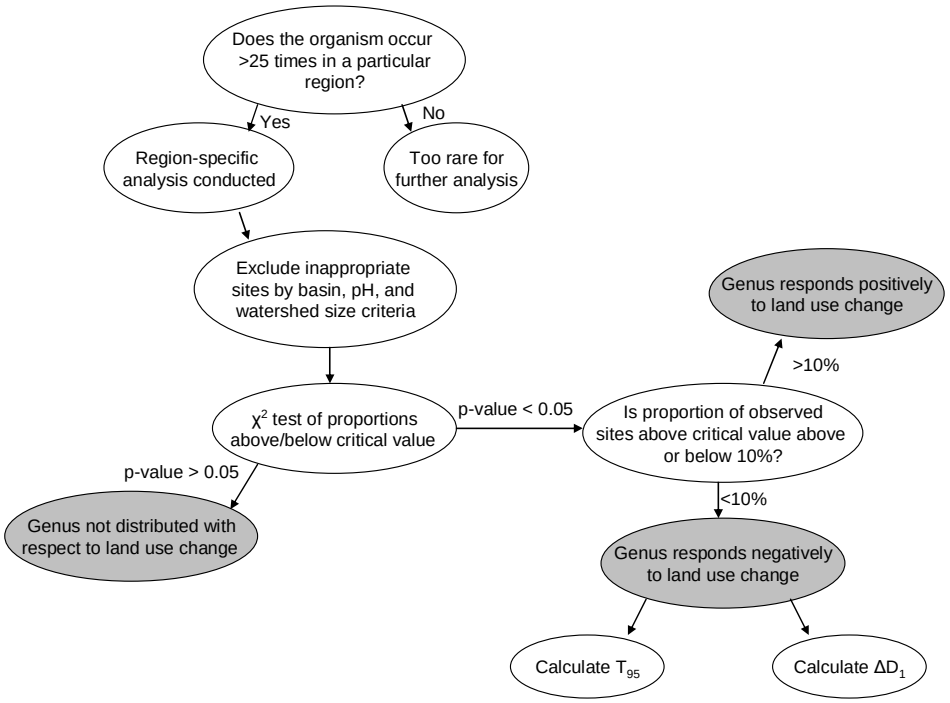

Figure 3. Flow chart representing the process conducted for determining taxon-specific response with respect to land cover change. Ovals with grey fill represent endpoints for the three potential relationships with land covers.

Acidic streams—The mid-Atlantic region of the United States receives the most severe acidic precipitation in the United States, and streams with naturally poor

buffering capacity are affected as result (Herlihy et al. 1993). Additionally, acidic mine drainage from coal mines in the Highlands region of Maryland may dramatically alter the chemical and biological properties of streams (Simmons et al. 2005, Merovich and Petty 2007). A water sample taken during macroinvertebrate collections and chemically analyzed for pH in a laboratory was used to filter out sites that were too acidic for each taxon. For each taxon, a quantile analysis of pH levels across sites where the organism was collected was performed, and all sites that fell below the 5% quantile of pH values were omitted from further analysis in both observed and expected sets of streams.

Major basin and stream size— We used a hierarchical filtering process to exclude watersheds where a taxon did not likely occur historically. To account for biogeographic effects, we also used a biogeographic filter to exclude watersheds where a species did not likely occur historically. Only watersheds where the species was collected at the Maryland 6-digit hydrologic unit code (17 major basins within the state, Heimbuch et al. 1999) scale were included for analysis. Sites below the minimum and above the maximum basin area size where each taxon was collected by the MBSS program were excluded as well.

Distribution with land cover change— Once pH-, biogeographic-, and size-inappropriate sites were excluded, the actual and expected occurrences of each taxon were compared in relation to land cover. For each respective region, the cumulative frequency distribution (CFD) of all sites arranged by percent land cover (i.e. agricultural, urban or ISC) was calculated. This 'expected' group included all sites where the taxon was and was not collected. The land cover percentage at the 90^{th}

percentile (termed the critical value) for the expected set of sites was determined and compared to the suite of the sites where the taxon was collected, hereby termed the 'observed' group. A chi-square goodness of fit test on the frequencies above and below the critical value was performed between the expected group (10% above and 90% below the critical value) and observed group (% above and % below). If the chi-square test showed no significant difference ($\alpha \geq 0.05$) between proportions, the land cover was assumed to have no relationship to the occurrence of the taxon. However, if the chi-square test resulted in a significant difference between frequencies, analysis of the CFD curves continued.

If a taxon's distribution was found to be significantly affected by land cover, two scenarios were possible. First, the taxon may have responded positively to the particular land cover, and populations were consequently more frequently observed in catchments with high percentages of agricultural, urban, or impervious land cover. Such was the case when the number of observed sites above the critical value was significantly higher than 10%. Alternatively, the taxon may be negatively affected by the particular land cover gradient. Here the number of occurrences above the critical value was significantly lower than 10% (in many cases 0%).

When a significant negative response occurred, two values were calculated to describe the severity of response. The T_{95} (i.e. 95% threshold) is the land cover value at which 95% of the occurrences fall below and represents the maximum percentage for a specific land cover in a catchment that could conceivably retain the taxon. The second value, D_1, estimates the point of divergence between the two CFD curves and represents the minimum detectable land use affect. Each cumulative frequency

quantile of land cover in the observed site group was matched and compared to the closest possible quantile in the expected stream group. Starting from zero, once the difference in percent land cover for the same quantile on both curves exceeded (and remained above) 1%, the curves were considered divergent and was assumed to be the point where the land cover negatively affects the taxon. Fig. 4 presents a graphical example of the critical value, T_{95}, and D_1.

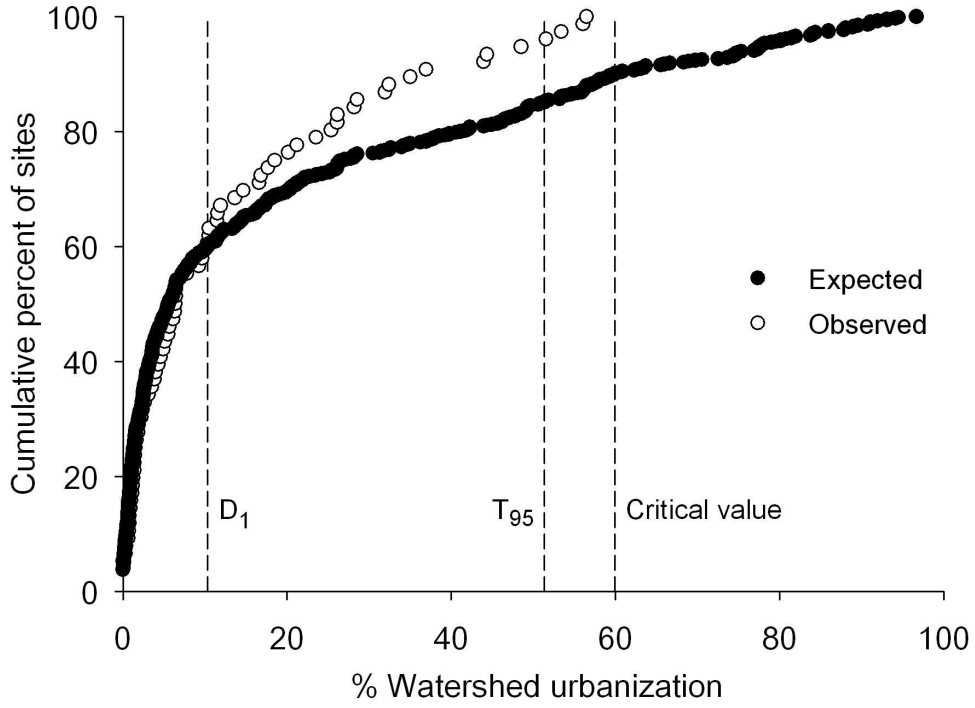

Figure 4. The effect of watershed urbanization on the distribution of *Nigronia* (Megaloptera: Corydalidae) in the Coastal Plain of Maryland. Each dot represents a sample. The three values calculated to determine the severity of response are shown as dashed lines

Results

Among the three regions, 180 benthic macroinvertebrate taxa were analyzed for distributions relative to land cover categories (see Appendices A through C for all

taxon-specific results and Table 2 for a summary of responses by land cover and region). The number of analyses conducted within each region differed, with 126 genera and 3 families analyzed in the Coastal Plain, 102 genera and 3 families analyzed in the Piedmont, and 77 genera and 3 families analyzed in the Highlands. Due to low levels of urbanization and ISC in the Highlands, only responses to agriculture were assessed in this region. All three hypothetical responses (no effect, positive distribution, negative distribution) with respect to land cover were observed (see Fig. 5 for examples of each). The responses of benthic organisms varied broadly by type of land cover and physiographic region.

Table 2. Summary of the taxa examined for a distributional relationship with land use change by region and cover type.

Land cover	Physiographic province	n taxa	Number (percent) of taxa with negative response	Number (percent) of taxa with positive response	Number (percent) of taxa with neutral response
Urbanization					
	Coastal Plain	129	57 (44.2)	13 (10.1)	59 (45.7)
	Piedmont	105	59 (56.2)	15 (14.3)	31 (29.5)
Impervious surface					
	Coastal Plain	129	59 (45.7)	12 (9.3)	58 (45.0)
	Piedmont	105	59 (56.2)	14 (13.3)	32 (30.5)
Agriculture					
	Coastal Plain	129	12 (9.3)	27 (20.9)	90 (69.8)
	Piedmont	105	1 (0.9)	13 (12.4)	91 (86.7)
	Highlands	80	24 (30.0)	11 (13.8)	45 (56.2)

Urbanization— In the Piedmont the majority of taxa responded negatively to urban land cover as well as nearly half of tested taxa in the Coastal Plain (Table 2). The magnitude of the response varied by taxonomic group. For instance, nearly all

Plecoptera responded negatively to catchment urbanization (89% in Coastal Plain and 100% in Piedmont), while less than a third of Chironomidae (from all tested

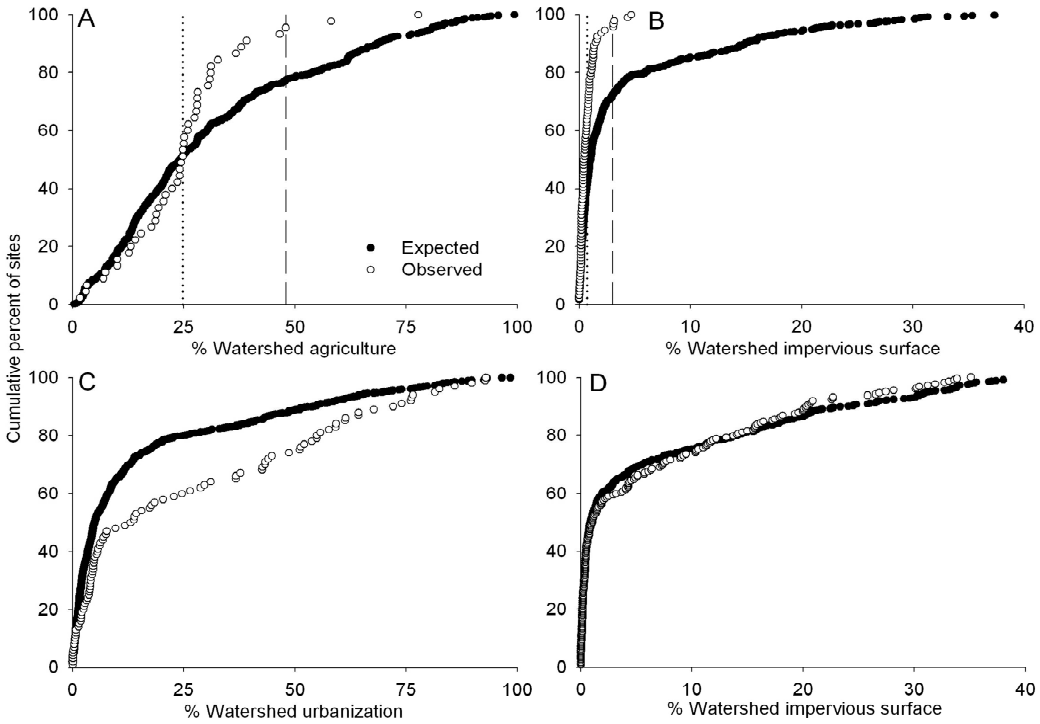

Figure 5. Examples of taxon-specific distributions in relation to land cover change. Relationships shown include (A) an example of a delayed negative response to agriculture (Plecoptera: Leuctridae: *Leuctra*) in the Coastal Plain, (B) a rapid negative response to impervious surfaces (Ephemeroptera: Heptageniidae: *Epeorus*) in the Piedmont, (C) a positive response to urbanization (Malacostraca: Crangonyctidae: *Crangonyx*) in the Piedmont, and (D) no relationship to impervious surfaces (Trichoptera: Hydropsychidae: *Cheumatopsyche*) in the Coastal Plain. When the relation to land cover is negative, the D_1 and T_{95} values are shown as dotted and long dashed lines, respectively.

subfamilies) were negatively affected in either physiographic province (Fig. 6). Some notable differences in group sensitivity to urban land use between physiographic provinces occurred. All Ephemeropterans were negatively affected by urban land cover in the Piedmont, yet in the Coastal Plain one-third (from various families) were tolerant of urban cover.

Similarly, all but one Coleopteran (*Stenelmis*) in the Piedmont was negatively affected by urban cover contrasted with only half of those tested in the Coastal Plain (*Agabus* and *Hydroporous* in the family Dytiscidae, commonly collected only in the Coastal Plain, were urbanization tolerant).

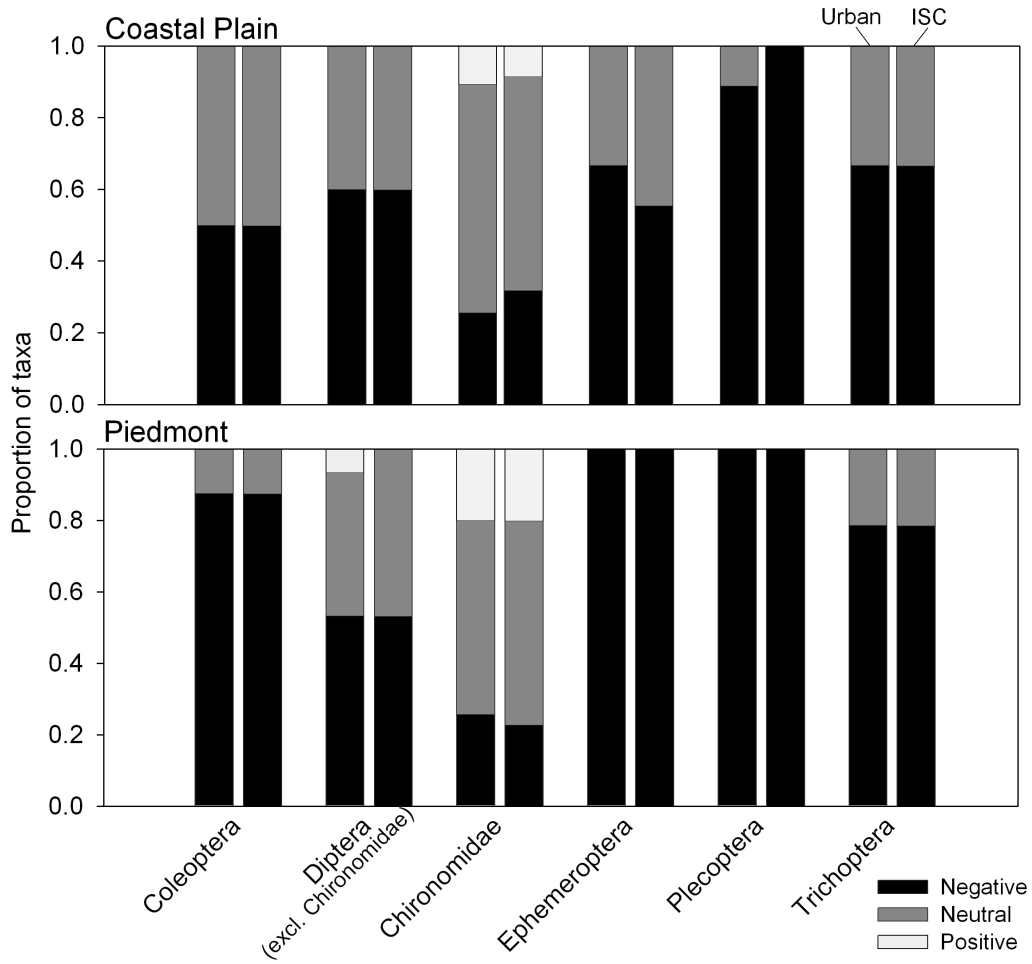

Figure 6. Summarized responses to urban land covers of some insect groups in the Piedmont and the Coastal Plain. For each taxonomic group, bars on the left represent the response to urbanization, bars on the right sum the response to impervious cover.

Regional differences were observed in specific values as well. Both T_{95} and D_1 values were typically greater for organisms inhabiting the Coastal Plain than those in the Piedmont. Many genera common to both the Coastal Plain and Piedmont also

responded differently between provinces, with consistently higher T_{95} and D_1 values in the Coastal Plain. Of the 51 urbanization-intolerant taxa collected in both physiographic provinces, 72% exhibited greater sensitivity to urbanization in the Piedmont (see examples of Plecoptera in Table 3). The majority of taxa negatively impacted by urbanization disappeared between 10-45% urbanization in the Piedmont, whereas in the Coastal Plain the majority disappeared at 15-60% urbanization (Fig. 7). In both provinces, however, no taxon had a T_{95} value greater than 60%. Thus once ~60% urbanization in a watershed is realized, apparently all taxa remaining in sites respond either neutrally or positively with respect to urbanization.

Table 3. Examples of urban and impervious surface (ISC) T_{95} and D_1 values for Plecoptera genera common to both the Piedmont and Coastal Plain. The number of times each genus was collected per province (n) is provided. A full listing can be found in Appendices A and B.

		Coastal Plain					Piedmont				
			Urban		ISA			Urban		ISA	
Family	Genus	n	D_1	T_{95}	D_1	T_{95}	n	D_1	T_{95}	D_1	T_{95}
Capniidae											
	Allocapnia	33	3.5	16.9	0.5	5.1	51	5.2	14.3	1.3	3.8
Leuctridae											
	Leuctra	55	3.6	47.2	1.5	10.6	45	1.0	31.7	1.2	12.3
Nemouridae											
	Amphinemura	150	6.5	47.0	1.2	15.0	310	1.7	26.7	1.2	5.9
	Prostoia	113	6.1	45.0	1.5	15.9	218	2.7	20.3	1.5	4.7
Perlidae											
	Eccoptura	61	3.6	26.1	0.6	5.7	42	7.2	40.0	4.6	9.9
Perlodidae											
	Isoperla	135	4.1	45.7	0.7	14.6	41	1.0	10.1	0.4	1.9
Taeniopterygidae											
	Strophopteryx	39	13.4	34.5	2.9	9.7	90	2.7	13.4	1.1	3.5

Some genera were more frequently collected in urbanized watersheds. Several Oligochaeta, Diptera, Odonata, and Gastropoda were found to be positively associated with urbanized land cover (Appendix A, Fig. 6). Proportionally, Oligochaeta was the largest group that responded positively to urban development (three-fifths and two-thirds of tested genera or families in the Coastal Plain and Piedmont, respectively).

Impervious surface cover— Organisms responded to impervious surface cover at much lower levels within catchments compared to urban cover. However, differences in T_{95} and D_1 values between physiographic provinces existed and were consistent with patterns observed for urban cover (Table 3, Appendices A and B). Taxa sensitive to impervious cover were generally lost between 2.5 and 15% cover in the Piedmont while sensitive taxa in the Coastal Plain possessed T_{95} values between 4-23% cover (Fig. 7). The proportions of major groups that were affected by ISC were similar to those observed for the urban cover gradient (Fig. 6), and the total number of taxa sensitive to impervious cover was similar to the number of urban-sensitive taxa (Table 2); in almost all cases if a taxon was negatively affected by urban development it was negatively affected by ISC (Appendices A and B).

Agriculture— Relatively few organisms were negatively impacted by agriculture (Appendix C); a strong majority of genera in all three regions showed no distributional response (Table 2). In the Piedmont and Coastal Plain, the number of genera that were positively associated with agricultural development exceeded the number negatively impacted. The Highlands region possessed the greatest number of taxa that were intolerant of agriculture, with greater than one-fourth of those tested

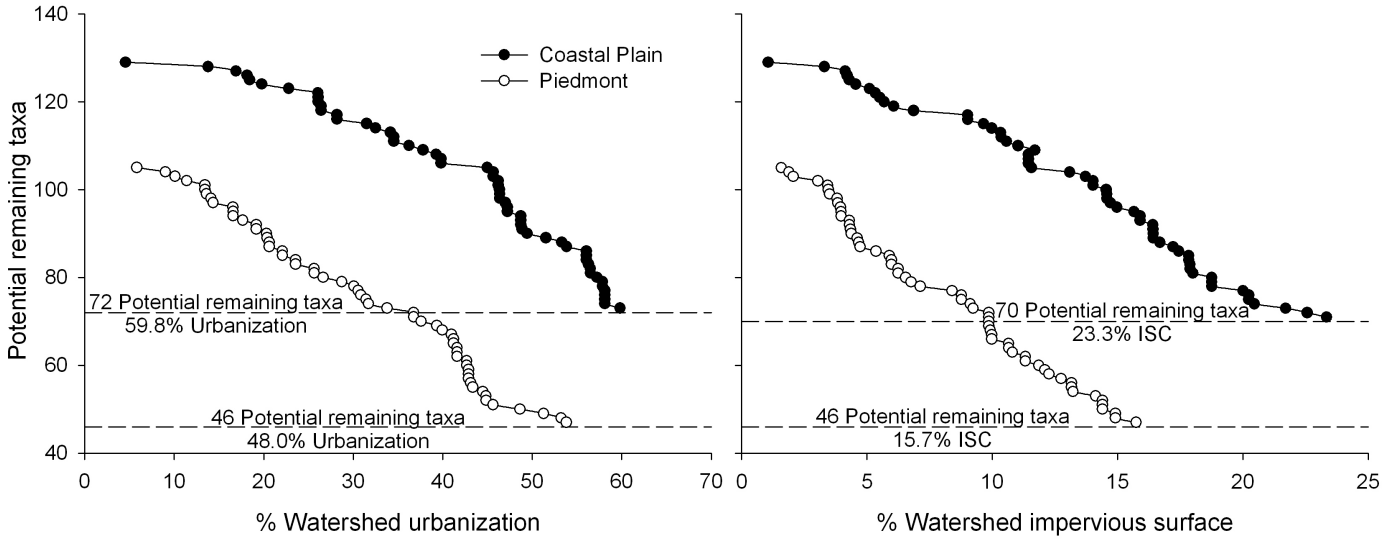

Figure 7. The number of taxa remaining given the distribution of urbanization and impervious surface cover as represented by T_{95} values by physiographic province. Each point represents a T_{95} value for a taxon collected ≥25 times; dashed lines denote where all urbanization- or impervious surface-sensitive species have been accounted for. The number of tolerant genera remaining after all sensitive genera have been extirpated is also provided.

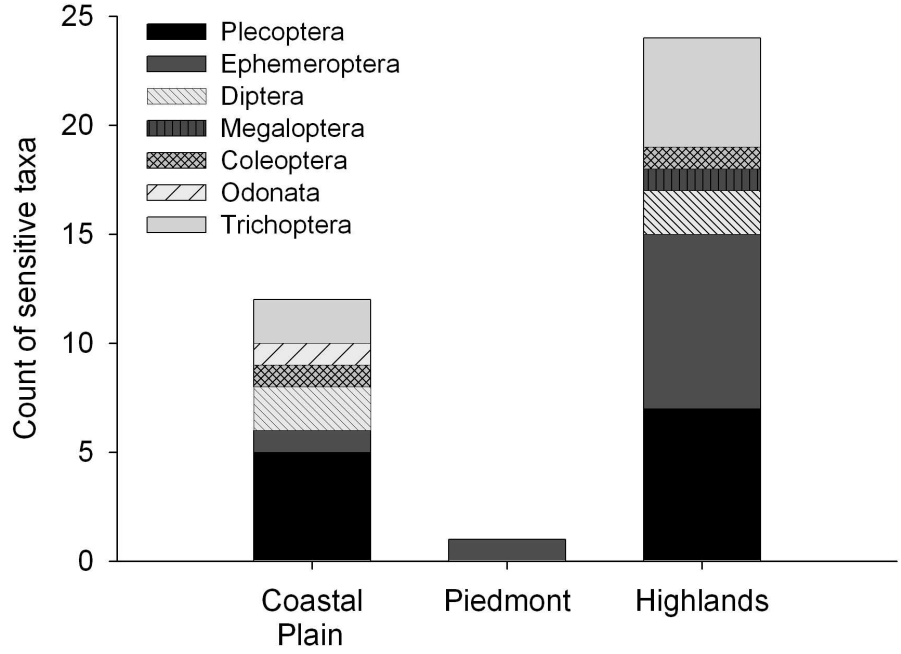

Figure 8. Summary (by physiographic region) of taxa that were negatively distributed with respect to watershed agricultural cover.

exhibiting negative responses. All organisms that were negatively associated with increasing agricultural development were insects, with genera in the order Plecoptera representing multiple families most consistently adversely affected (5, 1, and 7 agriculture-sensitive taxa in the Coastal Plain, Piedmont, and Highlands, respectively). Similar numbers of Ephemeropterans (8) and Trichopterans (5) from various representative families in the Highlands were negatively affected (Fig. 8).

Taxa that responded negatively to agricultural development were capable of tolerating higher levels of agriculture relative to those seen with urbanization; the lowest T_{95} score for agricultural development was ~21% (Plecoptera: Taeniopterygidae: *Oemopteryx* in the Highlands) compared to 4.6% for urbanization

(*Clinotanypus* in the Coastal Plain) and 1.6% for ISC (*Drunella* in the Piedmont). In contrast to the findings along urban gradients, many taxa present in agriculture-dominated watersheds included those in groups usually considered stressor sensitive, such as Plecoptera, Ephemeroptera, and Trichoptera (Appendix C), especially in the Piedmont province. For instance, both tested Plecopterans in the family Capniidae (*Allocapnia* and *Paracapnia*) were quite sensitive to urbanization and ISC (both possessed T_{95} ISC values of 3.8) but were significantly positively associated with high agriculture streams.

T_{95} and taxa rarity— To assess the influence of rarity of a taxon on the T_{95} values (i.e. more rare taxa possessing lower T_{95} values), we regressed T_{95} values of sensitive organisms against the collection frequency. Separate regressions were run for urban and ISC T_{95} values in the Piedmont and Coastal Plain, and agriculture T_{95} values in the Highlands. None of the relationships were significant (n =24-59, F=0.00-2.17, p=0.147-0.966).

Discussion

Our analytical approach identified a wide array of benthic macroinvertebrate responses, ranging from complete tolerance to acute sensitivity, along human altered land use gradients. The diversity of responses implies that our methodology is capable of identifying potential indicator taxa as well as differentiating sensitivity within indicators. The approach is straightforward and does not require permutation tests or computer intensive operations to arrive at relative sensitivity values among taxa. The method also is more robust to variations in sample size than techniques such as the Kolmorogrov-Smirnov test. While the analyses were targeted to benthic

macroinvertebrates, the method can be generalized to other taxa or even entire assemblages, and its use is not restricted to aquatic environments. The results are easily interpreted with decision points that can be adjusted up or down to account for uncertainty; T_{95} values estimate the degree of watershed development where the taxon is no longer expected to be collected, and D_1 values indicate the minimum detectable amount of development that may negatively affect a taxon. The difference between the two descriptor values also conveys meaning: a small range between the D_1 and the T_{95} indicates a rapid loss of particularly sensitive taxa while a large difference suggests that the taxon is capable of survival in altered watersheds, but will eventually disappear in highly altered watersheds.

The diversity and number of sensitive taxa in Maryland streams points to the presence of ecological thresholds. Our analyses suggest that threshold detection is scale dependent on a number of levels. Across the entire stressor gradient, clear thresholds exist in responses of individual taxa to urbanization, impervious surfaces, and agriculture (e.g., Fig. 5b). However, thresholds may not be detected if only a portion of a stressor gradient is analyzed, particularly if the portion is at the low-disturbance end. Although threshold responses were evident for individual taxa, scaling up by aggregating across taxa showed linear declines in richness (Fig. 7). Groffman et al. (2006) concluded that little consistent evidence for thresholds exists and that aquatic community degradation with land use may be linear, whereas others report threshold responses at 10-15% watershed impervious surface (Paul and Meyer 2001). Our findings support both contentions depending on the scale of analysis.

Differences in tolerance thresholds also appear to be influenced by spatial scale. We found substantial response differences to urbanization measures between the Piedmont and Coastal Plain for individual taxa and richness declines when aggregating across taxa. Although taxa loss was nearly linear across urban gradients in both regions (Fig. 7), losses occurred at much lower stressor levels along the gradients in the Piedmont. Furthermore, a substantial majority of urbanization-intolerant taxa found in both provinces exhibited greater sensitivity in the Piedmont. Increasing the spatial extent of analysis would have obscured differences between the regions as well as altered threshold responses of indicators. Similar differences between these two regions were reported for analyses using a mulitmetric approach for fishes by Morgan and Cushman (2005), who partially attributed the result to ineffectively constructed indices of biotic integrity. Later work adjusted the metrics to obtain a more homogeneous response to environmental stress between regions (Southerland et al. 2007). Our results suggest the differences are real, and the effects of urbanization may be less severe on stream biota in the Coastal Plain, but we have not identified specific mechanisms for the responses.

In contrast to urbanization, few taxa distributions were negatively affected by increasing agricultural land cover. Effects were most evident in the Highlands where agriculture has never been widespread, whereas only one taxon in the Piedmont responded negatively. The relative lack of response in the Piedmont and Coastal Plain may be due the centuries-long legacy of agriculture and settlement in these areas (Jacobson and Coleman 1986, Waisanen and Bliss 2002, Jackson et al. 2005) that may have eliminated the more agriculture-sensitive taxa decades ago. Such artifacts

of land use past (*sensu* Harding et al. 1998, Harding 2003) complicate inferences drawn from current conditions. Additionally, organisms with moderate sensitivity to stressors may have adapted to degraded environmental conditions (Lopes et al. 2006). The relationship is further complicated because agriculture-dominated watersheds in the Maryland Piedmont may possess high invertebrate diversity in streams (Moore and Palmer 2005), and agriculture generally appears to be less damaging to aquatic taxa than urbanization (Wang et al. 2000, Poff et al. 2006).

The broad classes of urban and agriculture are surrogates for the specific mechanisms that cause the loss of sensitive taxa from streams and thus form convenient yet relevant measures for analysis. Urbanization and associated impervious surfaces dramatically alter hydrologic regimes (Booth and Jackson 1997, Schuster et al. 2005, Konrad and Booth 2005), increase organic and inorganic pollutant concentrations (Lenat and Crawford 1994, Rogers et al. 2002, Chadwick et al. 2006, Morgan et al. 2007), promote prolonged geomorphologic adjustment (Wolman 1967, Pizzuto et al. 2000, Colosimo and Wilcock 2007), and cause shifts in temperature regimes (Klein 1979, Arnold and Gibbons 1996, Leblanc and Brown 1997). Agriculture may cause relatively less severe change, but may cause increased sedimentation (Cuffney et al. 2000, Donohue et al. 2006), elevated nutrient levels (Jones et al. 2001), shifts in water temperature dynamics (Wehrly et al. 2006), and altered hydrologic regimes (Poff et al. 1997, Poff et al. 2006). While specific stressors are important to benthic responses, analysis of individual stressors over large spatial scales will likely increase the noise, whereas surrogate measures such as urbanization can integrate the suite of correlated stressors.

A valuable application from our analysis is the catalog of macroinvertebrate responses to land use change (Appendices A-C). While an exhaustive comparison of existing indicators with thresholds determined by our technique is not the purpose of this paper, the reported sensitivities in the appendices can be used to assess if a given taxon or composite metric will be sufficiently sensitive to land use. Further, our response catalog can be used to forecast biodiversity losses for specific watersheds or to examine if some taxa may eventually become regionally threatened due to land conversion in the increasingly urbanized mid-Atlantic region (Brown et al. 2005, Grimm et al. 2008). Though our results should not be considered replacements for rigorous demographic assessments, the catalogue may form a useful starting point for management and conservation of a group of organisms often overlooked by mainstream conservation efforts (Master et al. 2000, Strayer 2006). Additionally, the catalog may be used to identify exceptional streams: if an urbanized stream continues to contain multiple sensitive taxa, the stream may be especially resilient to landscape change and would merit special attention.

The pre-analysis site filtering caused the suite of watersheds used for landscape sensitivity assessments to differ for each taxon. Watershed size and acidity are largely uncorrelated with landscape stressors in the MBSS dataset (Utz et al., in press). Therefore the hierarchical filtering process largely did not affect the distribution of landscape stressor values among tested taxa, and inter-specific comparisons of thresholds may be made with reasonable confidence. We specifically targeted only those sites where an organism should occur in the absence of landscape stressors. Including additional sites would have been inappropriate: watersheds not meeting the

range of the filtered environmental conditions would not support a taxon. Very few invertebrates were limited to a small number of major basins. Geographically restricted taxa that were collected by the MBSS program tend to be collected with reduced frequency and therefore were not assessed.

Our analytical approach did not address certain factors that may complicate how land use change affects stream ecosystems. We tested land use classes independently though multiple landscape stressors may simultaneously impact streams. While our analysis did not account for interactions between land uses, we believe the effect was not substantial given that agriculture and urban land uses in the Piedmont and Coastal Plain were negatively correlated with one another, and only a weak positive correlation existed in the Highlands (Table 1). Another source of uncertainty comes from the nine year observation period for the invertebrate data (1995-2004) applied to the land use data for only 2001. The land use present during a given collection may not be exactly congruous to what was assessed for what is likely a small number of watersheds. We were limited to the availability of the 2001 data and must assume that it is approximates the actual land uses during the year of collection. In addition, local attributes such as instream habitat and riparian condition undoubtedly influence taxa occurrences (Sponseller et al. 2001, Sandin 2003, Barker et al. 2006) and will introduce some noise into the results. Such uncertainties should make the listed sensitivities more conservative (more difficult to detect an effect) because some sites with low amounts of urban or agriculture will not have taxa due to unfavorable local conditions.

In summary, our approach was able to identify ecological thresholds and order taxa sensitivity across a range of land uses. While specifically targeted to benthic macroinvertebrates here, the technique may be applied to any organism distributed along a stressor gradient provided that a large enough sample size and range of stressor values are available. We found substantial differences in sensitivity of benthos to landscape change between streams located in adjacent regions, highlighting the importance of choosing the appropriate scale when assessing ecological responses to land use change. The findings also point to the possibility that benthic macroinvertebrates are generally more sensitive to urban land uses in Piedmont compared to Coastal Plain streams. Given the ongoing human population growth and land conversion throughout the mid-Atlantic region, our results cataloging taxa sensitivities should prove useful for future development of assessment metrics and land use planning to help minimize biodiversity loss and ecosystem degradation.

CHAPTER III

TAXON-SPECIFIC RESPONSES OF FISHES TO LAND COVER CHANGE

(At the time of dissertation submission, this chapter has been accepted for publication in the journal *Biological Conservation*, titled "Regional differences in patterns of fish species loss with changing land use" by R.M. Utz, R.H. Hilderbrand, and R.L. Raesly.)

Land use change ranks as the dominant driver in the global biodiversity decline across multiple biomes and ecosystems (Sala et al., 2000), yet the relationship may be nuanced and complex. Differences between even adjacent ecoregions may render one locale more sensitive to species loss from the same form and magnitude of land use change than another, even when species composition is similar between regions (Huggett, 2005). Species loss may occur decades or centuries after patch isolation and fragmentation (Hilderbrand, 2003; Lindborg and Ericksson, 2004; Vellend et al., 2006), making its true magnitude difficult to detect. Further, invasions of non-native species and/or species compositional shifts from sensitive to tolerant taxa in degraded habitats may obscure responses by mitigating biodiversity declines when comparing commonly used measures such as species richness against gradients of land use change (Walters et al., 2005).

A broad suite of land use associated stressors influences stream biodiversity as streams are tightly linked to past and present activity in their watersheds (Harding, 1998; Gergel et al., 2002). Substantial physicochemical degradation in streams may occur at multiple temporal and spatial scales due to land use change (Allan, 2004), and these in turn may influence distributions of aquatic organisms. Common stressors include altered hydrologic regimes (Konrad et al., 2005), elevated nutrient and pollutant loads (Jones et al., 2001; Sprague and Nowell 2008), shifts in temperature

extremes and variability (Price and Leigh, 2006; Wehrly et al., 2006), and reductions in substrate and habitat heterogeneity (Waters, 1995; Jones et al., 2001; Sutherland et al., 2002). A substantial number of aquatic taxa are imperiled due to such stressors (Sala et al., 2000; Wilcove et al., 2000; Abell 2002; Strayer 2006). In North America, 39% percent of all described freshwater fish species are considered imperiled in part due to land use change, a number that has nearly doubled in the past twenty years (Jelks et al. 2008). Though comprehensive species status assessments in other regions are often less complete, estimates of imperilment are consistently alarming. For example, as much as 50% of the Mediterranean and Malagasy freshwater fish fauna are in danger of extinction, partially as a result of forest clearing, agriculture, and urban expansion (Darwall et al., 2008).

Due to the multivariate nature of land use associated stressors, broad landscape classifications may be effective surrogates for quantifying degradation. Physicochemical changes are often correlated with one another in developed catchments (Gergel et al., 2002; Joy and Death, 2002; Short et al., 2005; Potopava et al., 2005, Meador et al. 2008). For example, urbanization may simultaneously elevate water temperatures, substantially alter the hydrologic regime, and increase pollutant loads, each of which may independently or interactively impact aquatic organisms (Walsh et al., 2005). Therefore, at large spatial scales, broad land cover classes stand as useful measures of disturbance and allow for analyses of species sensitivity over the entire stressor gradient. Such landscape-scale approaches complement analyses of species sensitivity to component physicochemical stressors (Eaton and Scheller,

1996; Pollard and Yuan, 2006) to comprehensively assess the conservation needs of threatened taxa.

Geoclimatic variability among ecoregions also may complicate the relationship between land use change and biodiversity. Physicochemical changes induced by urbanization such as hydrologic regime shift (Poff et al., 2006) and elevation in pesticide concentrations (Sprague and Nowell, 2008) may vary substantially among geoclimatic locations along analogous urban land use gradients. Similarly, nutrient concentrations may not be uniformly affected by agricultural intensity even among adjacent physiographic settings (Jordan et al., 1997b; Liu et al., 2001). Biological assemblages may therefore respond differently to the same landscape stressor among ecoregions. For instance, in the Mid-Atlantic United States, fish and macroinvertebrate biotic integrity metrics (Morgan and Cushman, 2005; Goetz et al., 2009) as well as individual macroinvertebrate taxa (Utz et al., 2009) show heightened sensitivity to urbanization in the eastern Piedmont physiographic province relative to the Coastal Plain. Yet despite explicit calls for further inquiry into physiographic mediation in landscape-stream interactions (Walsh et al., 2005), interregional comparisons of landscape stressor sensitivity remain scarce.

Given the rapid expansion of urban land (Brown et al., 2005) and ongoing degrading impact of agricultural practices on streams (Barker et al., 2006) in the eastern United States, we sought to quantify how fishes are distributed along land use gradients and whether such distributions differ between distinct, yet adjacent, geoclimatic regions. Our study area was the state of Maryland in the Mid-Atlantic region of the United States, a region experiencing rapid urban and exurban growth

with substantial fish diversity (including 31 species considered vulnerable to local extirpation). Study objectives included: 1) quantify sensitivity (i.e. risk of population reduction and extirpation) of fish taxa to land uses by analyzing fish distributions along urban and agricultural land use gradients; 2) identify both general and species-specific differences in patterns among regions; and 3) address landscape-scale conservation implications for current and future species of concern.

Methods

Study area

The state of Maryland encompasses about 32,000 km^2 of land in the mid-Atlantic United States. Nearly all watersheds in the state drain to the Chesapeake Bay; a small area (~1,100 km^2) empties to the Ohio River in the western portion of the state and some tributaries (430 km^2 area) drain directly to the Atlantic Ocean on the eastern shore. Three general geoclimatic regions are found in the state: the Coastal Plain physiographic province, the Eastern Piedmont physiographic province (hereafter Piedmont), and the Highlands (a conglomerate of the Appalachian Plateau, Ridge and Valley, and Blue Ridge physiographic provinces, Fig. 9; Omernick, 1987).

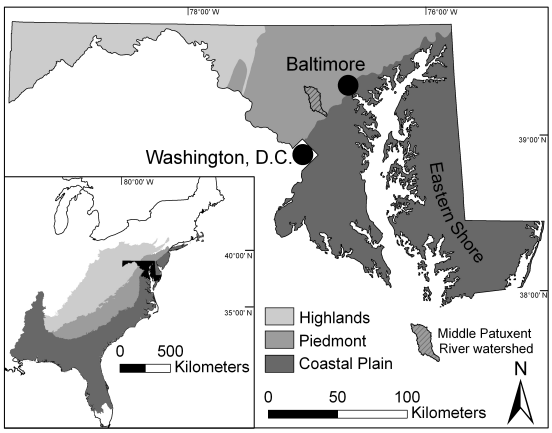

Figure 9. Map of the state of Maryland and the eastern United States illustrating the physiographic regions delineated for species-specific analyses.

Stream physicochemistry and geomorphology varies considerably among these three regions (Table 4). Topographic relief typically decreases on a west-to-east gradient from the Highlands to the Coastal Plain. As a result, mean channel slopes decreases and percent wetland cover increases categorically among regions from west to east. Climatic variability influences stream temperature such that the warmest streams are found in the Coastal Plain and coolest in the Highlands. Geologic variation among the three regions alludes to substantial differences in sediment regimes. Basement rock in the Coastal Plain is buried by unconsolidated siliclastic sediment ten to hundreds of meters thick (Ator et al. 2005); stream sediments consist of a heterogeneous mix of cobble, sand, silt and clay.

Table 4. Means and ranges (in parentheses) of study watershed attributes delineated by region.

Variable	Coastal Plain	Piedmont	Highlands
Physicochemical			
Size (km^2)	34.9 (0.1-379.9)	38.2 (0.1-429.5)	55.0 (0.3-424.3)
Slope	0.4 (0.1-4.5)	0.9 (0.1-10.5)	1.4 (0.1-18.0)
pH	6.7 (4.0-9.1)	7.5 (6.3-9.6)	7.4 (4.9-8.7)
Mean summer temperature* (^oC)	21.0 (15.5-28.5)	19.4 (12.8-27.9)	18.1 (12.0-24.6)
Land cover (%)			
Forest	38.6 (0.1-100)	26.4 (0.0-98.5)	69.5 (0.0-100)
Wetlands	3.2 (0.0-49.2)	1.1 (0.0-14.2)	0.5 (0.0-4.8)
Agriculture	40.4 (0.0-99.4)	59.0 (0.5-100)	22.2 (0.0-91.1)
Urban	16.3 (0.0-96.7)	12.9 (0.0-98.5)	7.1 (0.0-80.7)

*-Derived from a subset of round two (2000-2004) MBSS sites; data loggers were typically deployed June 1-September 1.

Siliclastic and carbonate bedrock dominates in the Highlands while Piedmont bedrock is primarily composed of gneiss-schist; basement rock in both provinces is typically overlain by a 0.5-2m thick layer of soil (Swain et al. 2004). Highland and Piedmont stream sediments range from boulder to cobble, with finer grains on average found in the Piedmont. Piedmont streams are highly buffered, while tannic wetlands and a lack of buffering bedrock renders Coastal Plain streams the most acidic in the study region.

Biological data

Data were derived from rounds one (1995-1997) and two (2000-2004) of the Maryland Biological Stream Survey dataset (MBSS; Klauda et al., 1998). The MBSS is a statewide stream monitoring system with > 2,000 site collections. The survey uses a probability-based design to maximize representativeness of sites. Each wadable 75m stream reach within the state has a non-zero probability of being selected over a three year sample frame that is stratified by major river basins. No specific watershed size criteria was applied to filter sites, however >99.5% of those sampled were fifth Strahler-order or smaller ($\leq$282 km^2; Knighton, 1998) and mean catchment areas among sites in the three regions were similar (Table 4).

Fishes were collected during summer baseflow using equal effort, two-pass depletion electrofishing (Kazyak, 2001). The top and bottom of each section were blocked using nets to prevent fish movement during sampling. All fishes were identified to species. A number of water quality attributes (including pH) were measured at each site during summer fish sampling. Further detail concerning sampling of fish and water quality may be found in Kazyak (2001). Data analyzed in

the current study were derived from 2,227 fish collections, of which 528 were sampled more than once (271 of these were sampled twice).

Land cover data

For each site, watershed boundaries upstream from each sampling site were delineated using a flow corrected, 30 m resolution National Digital Elevation dataset (USGS, 2008), and the respective land covers from the 2001 National Land Cover Database (NLCD) were extracted in a GIS. To simplify analyses of catchment land cover, land cover designation was limited to Class-I categories (see USEPA, 2008 for a full description of all classes). Urban land represents low-, medium-, and high-intensity developed land along with open space urban development. Agricultural cover represents the sum of the pasture/hay and row crop categories. The area of each summed category (urban and agricultural land cover) was divided by the area of each watershed to estimate the percentage of developed and agricultural land. The 2001 NLCD dataset also includes an estimate of percent impervious surface cover (ISC) from 0 to 100; the total percent of impervious surface covering each watershed was calculated from this layer. Though urban cover and ISC are strongly correlated (Pearson correlation coefficients=0.91-0.96 in sample sites among the three regions, $p<0.0001$ in each case), we ran analyses on both coverages for several reasons. Both classes of land use are commonly used to quantify environmental impacts on streams and we wished to provide quantitative data on each to ease comparisons of our findings to related work. Additionally, the classes may account for somewhat different stressors. For instance, elevated nitrogen concentrations in urban streams may largely originate from sewage and fertilizer derived from structurally pervious

urban areas rather than storm flow delivered by impervious surfaces (Groffman et al., 2004). We therefore wished to determine if any consistent differences were found in fish sensitivity between the two classes.

The two major metropolitan regions of Maryland (Baltimore and Washington, D.C.) are located at the border of the Coastal Plain and Piedmont (Fig. 9). As a result, the degree of urban land cover is similarly divided between the two regions, a trend reflected in the distribution of urban land in watersheds sampled by the MBSS program (Utz et al., 2009). In both the Coastal Plain and Piedmont, agriculture and urbanization are more negatively correlated with one another than either is with natural cover (Utz et al., 2009). Though urbanization and agriculture are positively correlated in the Highlands, urban cover is rare in the region. Further, relationships between watershed size and land use intensity (agricultural or urban) are absent or weak. Among the three regions and two classes of tested land use, five out of six correlations between watershed size and land use are not significant (Pearson correlation p-values=0.0543-0.6206). Watershed size is correlated with urbanization in the Piedmont, but only weakly (Pearson correlation coefficient=-0.0834, p=0.0154).

Statistical analysis

Prior to the analysis of distributions, we used a filtering process (Fig. 10) to include only sites expected to possess a species in the absence of landscape stressors. Low pH from atmospheric deposition and mine drainage may limit many fishes in the mid-Atlantic (McClurg et al., 2007). For each species, a quantile analysis of pH levels for species' occurrences identified sites that fell below the 5% quantile of pH and

were omitted from further analysis. We also used a biogeographic filter to exclude watersheds where a species would not be expected to occur naturally due to catchment boundaries and/or spatial limitations of distributions. Only watersheds

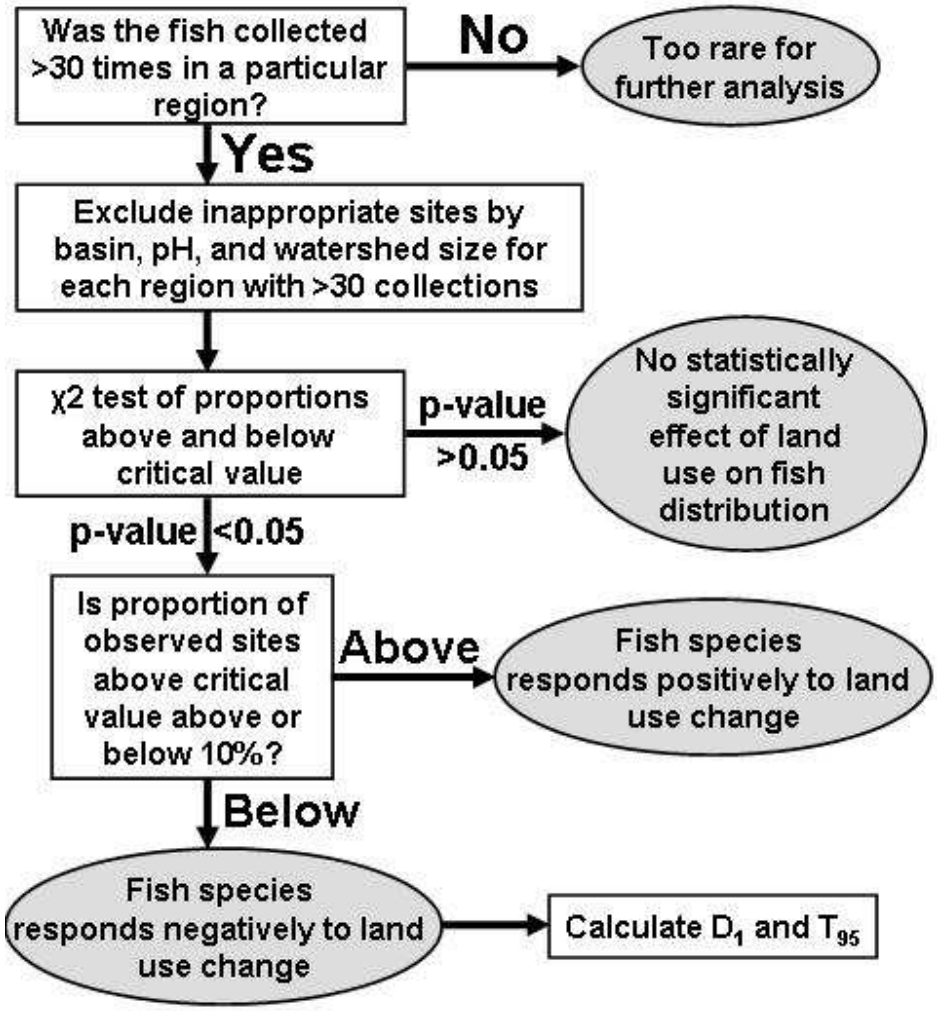

Figure 10. Flow chart representing the process conducted for determining species-specific response with respect to land cover change. Ovals with grey fill represent endpoints for the three potential relationships along land use gradients.

where the species was collected among the 18 major basins within the state (shown in Heimbuch et al., 1999) were included for analysis. We also removed sites located in the Eastern Shore for four species with relict populations there (*Catostomus*

commersoni, *Clinostomus funduloides*, *Notropis procne* and *Rhinichthys atratulus*; Jenkins and Burkhead, 1994). If a fish was biogeographically restricted to basins without substantial urban cover, we did not perform distributional analyses (this occurred for 5 fishes in the Coastal Plain and 2 in the Piedmont). Sites below the minimum and above the maximum basin area size where each species was collected by the MBSS program were excluded from further analysis. These large-scale filters (*sensu* Poff, 1997) typically account for a substantial amount of variation in lotic community composition at the landscape scale (Hawkins et al., 2000; De Zwart et al., 2006; Kennard et al., 2006) and thus were considered adequate to select the appropriate watersheds of analysis for each species. A number of other factors such as riparian or instream habitat, water quality, and temperature may potentially affect the abundance and distribution of stream fishes. Yet such variables are likely to be impacted by land use change and were therefore considered inappropriate for the preliminary filtering process.

We implemented a cumulative frequency distribution (CFD) analysis that compared the distribution of land cover at the sites where the organism was collected to the distribution where the organism would be expected if the effects from land use did not (positively or negatively) influence the species. Our main objective was to quantify species sensitivity to land use; we therefore used land cover classes as univariate environmental stress variables that are surrogates for the physicochemical responses which are multivariate and interactive. Though multivariate approaches are often used for similar large-scale analyses, our goal was to identify response thresholds to land uses rather than estimate component contributions of stressors to

fish species occurrence. Other factors not related to or influenced by land use (such as interspecific interactions) may influence fish community structure and population abundance. The CFD approach assumes that such factors not accounted for by the filtering process described above are spatially independent of land use. One advantage of using cumulative frequencies in concert with landscape-scale filtering is that species need not be present at every site where suitable habitat is available. Rather, the distribution of sites where a taxon was collected is compared to those where it is expected (inclusive of observed sites) with respect to a land use gradient. Thus rare and common species are treated equally. Because of the considerations above, our approach is meant to complement, rather than replace, related multivariate studies exploring environmental sensitivity of fishes as we are asking a different question.

To perform the CFD analysis once pH-, biogeographic-, and size-inappropriate sites were excluded, the actual and expected occurrences of each species were compared in relation to land cover. Within each physiographic region, the CFD of all sites arranged by percent land cover (i.e., agricultural, urban or ISC) was calculated. This 'expected' group included all sites where the species was and was not collected. The land cover percentage at the 90^{th} percentile (termed the critical value) for the expected set of sites was determined and compared to the suite of the sites where the species was collected, hereby termed the 'observed' group. Two observed CFD curves for each species were constructed: 1) a presence/absence curve where each occurrence was equally weighted and 2) an abundance-weighted (by number of

individuals collected at each site) curve where each occurrence was assigned a value based on the formula:

% = 100*(# of species A at specific site) / (# of species A collected across all sites).

The abundance-weighted analysis was used to detect if land use affected trends in population size, which may be a more subtle response than outright population loss. A Chi-square goodness of fit test on the proportions above and below the critical value was performed between the expected group (10% above and 90% below the critical value) and observed group (% above and % below). Since only two proportions were tested between stream sets, all such tests had one degree of freedom despite varying numbers of observed and expected sites among species. If the analysis showed no significant difference ($\alpha > 0.05$) between proportions, the land cover was assumed to have no relationship to the occurrence of the species. However, if the test did find a significant difference, analysis of the CFD curves continued.

If a species' distribution was found to be significantly affected by land cover, two scenarios were possible. First, the species may have responded positively to the particular land cover, and populations were consequently more frequently observed in catchments with high percentages of agricultural, urban, or impervious land cover. Such was the case when the percentage of observed streams above the critical value was significantly higher than 10%. Alternatively, the species may be negatively associated with the particular land cover gradient. Here the percent occurrence or abundance above the critical value was significantly lower than 10% (in many cases 0%).

When a significant negative response was detected, two values were calculated to describe the severity of response. The first was the 95th percentile of land cover in the observed stream set, termed the T_{95} (i.e., 95% threshold). This was considered the maximum percentage for a specific land cover in a catchment that could conceivably retain the species. The second calculated value estimated the point of divergence between the observed and expected CFD curves and is considered to be the minimum detectable effect, or the D_1. Each quantile (specific cumulative frequency) of land cover in the observed site group was matched to the closest possible quantile in the expected stream group. The percent land cover values of both groups were then compared by matched quantile, starting from zero. Once the difference in percent land cover for the same quantile on both curves exceeded (and remained above) 1%, the curves were considered divergent. At this point, the land cover percentage on the observed group curve was assumed to be where the land cover could negatively affect the species. Fig. 11 presents a graphical example of the critical value, D_1 and T_{95}.

In our approach we sought to quantify sensitivity using both presence/absence and abundance data and allow for comparisons of sensitivity at both scales. The substantial variation in collection frequency among fish species required that analyses were robust to species rarity. Values representing sensitivity (D_1 and T_{95}) were selected to represent the upper bound of land use tolerance (T_{95}) and minimal detection of effect (D_1), rather than the inflection point of most rapid loss in abundance or probability of occurrence. All three quantitative values (the critical value, D_1 and T_{95}) were, to some degree, arbitrarily selected to descriptively depict

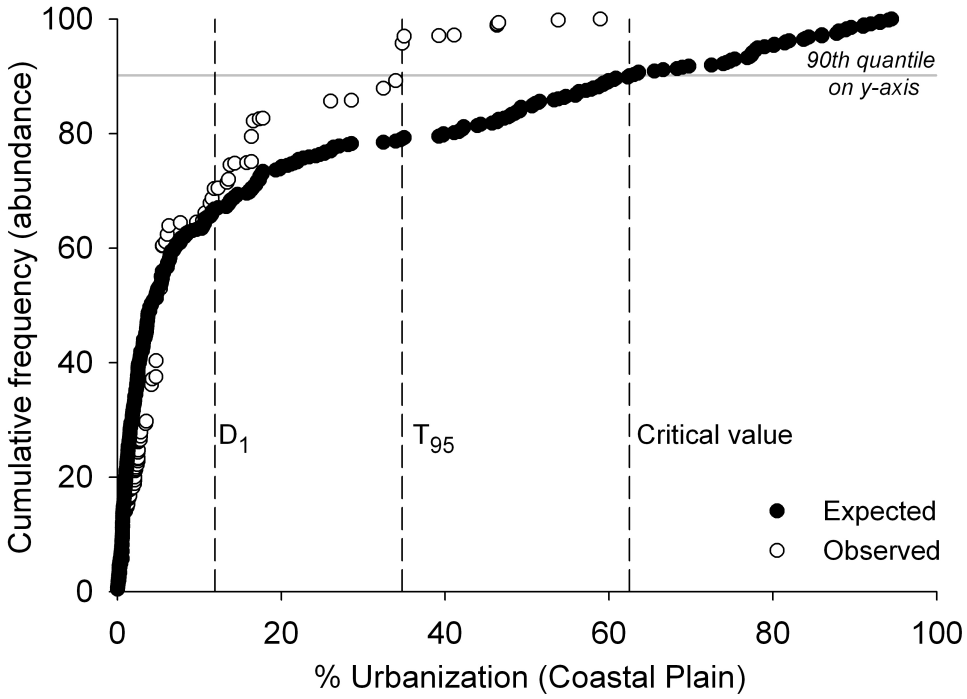

Figure 11. Cumulative frequency distribution of margined madtom (*Noturus insignis*) abundance and expected sites along an urban land use gradient in the Coastal Plain. All values used to quantify the distributional response are illustrated as dashed vertical lines; the 90th quantile on the y-axis (used to calculate the critical value) is also shown as a horizontal grey line.

species sensitivity. Those implementing our methodology in future work may adjust the reported values to derive more conservative or moderate estimates of species sensitivity.

We also summarized species responses based on taxa with deemed in greatest conservation need (GCN; taxa considered imperiled by the Maryland Department of Natural Resources) for fish with collection frequencies high enough to permit analyses. GCN status was designated by the state of Maryland (Kazyak et al. 2005) with the exception of American eel *Anguilla rostrata* (listed as a GCN species due to widespread population decline, Haro et al. 2000).

Sensitivity analyses

One concern pertaining to our analyses was that species rarity may artificially inflate landscape sensitivity due to the limited distribution of infrequently collected species. We therefore ran linear regression models relating the abundance-T_{95} values of sensitive fishes to species sample size by region and land use class (urbanization and agriculture) to assess if patterns of land use sensitivity was influenced by collection frequency.

We also performed a methodological sensitivity analysis on five species by randomly selecting 80% of the expected site pool, conducting the CFD analysis, and repeating the procedure for 1000 iterations. The mean chi-square p-value derived from this Monte Carlo randomization procedure was compared to the one derived by performing the analysis on the full expected site dataset. Five Coastal Plain species (*Aphredoderus sayanus*, *Esox niger*, *Lepomis auritus*, *Noturus insignis*, and *Rhinicthys atratulus*) were assessed using this procedure to determine if the statistical outcome (whether or not a species responded positively or negatively to urbanization) shifts when random subsets of expected sites are modeled in the CFD approach versus when using the full dataset.

Forecasting biodiversity

We spatially modeled both the status of an urban-sensitive fish and the projected loss of species richness in a Piedmont watershed as an example of biodiversity forecasting using D_1 and T_{95} values. Exurban growth in the Middle Patuxent River, a 150 km^2 tributary of the Patuxent River (Fig. 9), is likely to be particularly acute as the watershed is situated between the two metropolitan areas of Maryland. Urban land

use for the year 2030 was approximated using a spatially-explicit projected housing density model (Theobald 2005). Any cell with ≤0.7 hectares (1.7 acres) of land per unit of housing was classified as urban and integrated into the 2001 NLCD land use grid. The resulting layer projected urban land use based on the expansion of (medium to high density) residential urban land in 2030 and commercial/industrial urban cover during 2001. A suite of subwatersheds was derived by dividing the Middle Patuxent perennial stream network into sixty-five approximately equally spaced reaches, and percent urban cover was calculated for each.

The likelihood of extirpation and population status for the common, but urban-sensitive, fallfish (*Semotilus corporalis*) was forecasted in each subwatershed. Urbanization-driven extirpation and population reduction likelihood (using presence/absence and abundance analyses, respectively) was deemed negligible if urban development in the subwatershed was below the D_1 value, moderate if between the D_1 and T_{95} values, and high if greater than the T_{95} value. Only watersheds large enough (based on MBSS sites where the species was collected) to support fallfish were assessed.

Ichthyofaunal biodiversity was also forecasted using presence/absence D_1 and T_{95} values. Twenty two fish species assessed for land use sensitivity were collected in the Middle Patuxent River by the MBSS program; 11 of these 22 are urban-tolerant. Maximum potential diversity was spatially modeled in two forms: least sensitive, which assumed subwatersheds would support a sensitive fish if urban cover fell below the T_{95} value, and most sensitive, where sensitive fish were extirpated if subwatershed urbanization exceeded their D_1 value. Species were only included in a

subwatershed if it exceeded the minimum watershed size where the fish was collected.

Results

Distributions of 54 freshwater fish species across the three regions were tested against land use gradients (Appendices D, E and F and Table 5). Due to a lack of urbanization only agriculture was assessed in the Highlands region. Land use sensitivity of ichthyofauna varied substantially among both regions and classes of land use. We discovered the presence of all three hypothetical responses (negative, neutral, and positive associations) to land use gradients (see Fig. 12 for examples of each). In some cases no response was detected when presence/absence CFD curves were compared, but differences were evident for abundance-weighted data (Fig. 12a). Additionally, while some taxonomic groups exhibited a uniform response to a given land use gradient (cottids and percids), many congeners responded heterogeneously (Appendices D, E and F). For example, the ictalurids *Noturus* and *Ameirus* had both sensitive and tolerant species to given land uses.

Urbanization and ISC

Urban and ISC gradients exerted a pronounced effect on the distributions of fishes in the Coastal Plain and Piedmont overall, though responses often differed substantially between the regions (Fig. 13). In the Piedmont, a majority of fish species (26 out of 36 when abundance-weighted) were negatively affected along an increasing urban gradient; no species were collected more frequently or in greater numbers in urbanized watersheds (Table 5, Fig. 13). When presence/absence data were analyzed, the majority of urbanization-sensitive species possessed T_{95} values

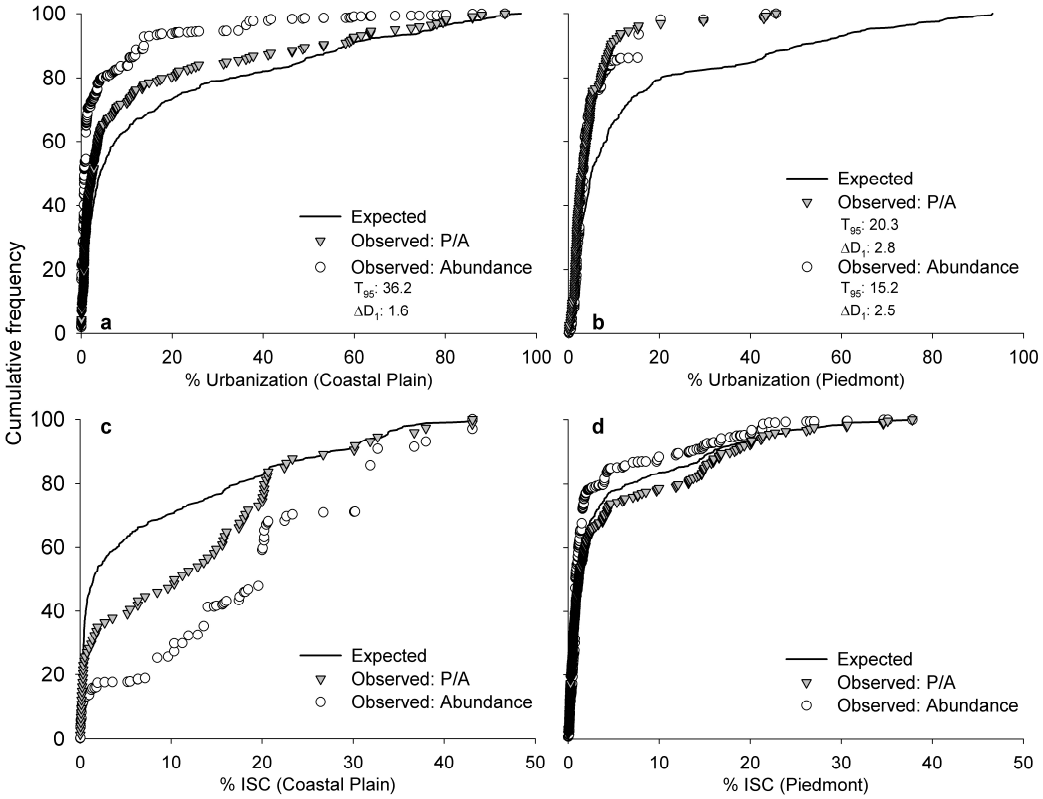

Figure 12. Examples of varying species-specific distributions along urban and impervious surface (ISC) gradients. When the observed curves were found to be significantly different than the expected, the T_{95} and D_1 values are listed in the legend. Shown are examples of (a) no significant difference in the presence/absence curve but a negative response of abundance along an urban gradient of golden shiner (*Notemigonus chrysoleucas*) in the Coastal Plain, (b) a rapid, negative response relative to an urbanization gradient for both presence/absence and abundance curves of Piedmont river chub (*Nocomis micropogon*), (c) evidence of a positive association with impervious surface cover in Coastal Plain green sunfish (*Lepomis cyanellus*), and (d) no apparent response of either curve along an impervious surface gradient in Piedmont American eel (*Anguilla rostrata*).

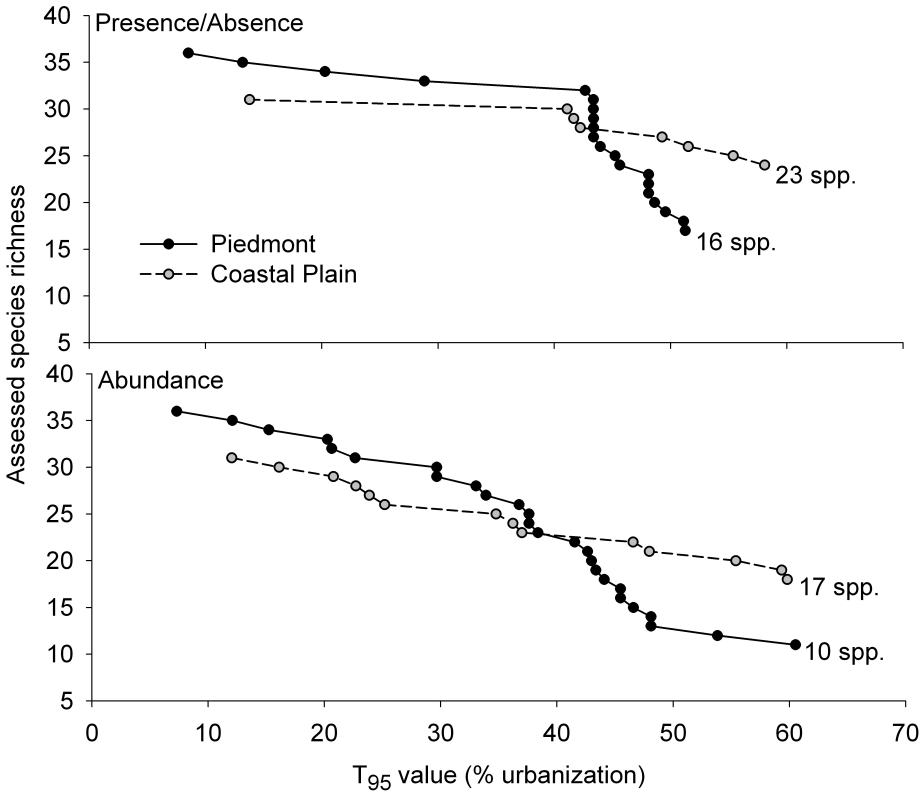

Figure 13. Decline in region-specific species richness (those common enough to allow assessment) along a watershed urbanization gradient represented by the distribution of T_{95} values of Coastal Plain and Piedmont fishes. The number of species that did not show a significant deviance or responded favorably to urbanization is listed at the far right of the curve.

between 40-55%. In contrast, T_{95} values for abundance-weighted data ranged relatively evenly between 8-60% (Fig. 5). River chub (*Nocomis micropogon*), rosyface shiner (*Notropis rubellus*), and brook trout (*Salvelinus fontinalis*) were found to be most sensitive, possessing T_{95} values between 6-20%. Sculpin (Cottidae, genus *Cottus*) and darters (Percidae, members of the genus *Etheostoma*) were also consistently sensitive to urban gradients. Several species such as the golden shiner (*Notemigonus crysoleucas*- Fig. 12a) exhibited no response along the urban gradient

when presence/absence data were considered but were found to be sensitive when curves were abundance-weighted

Fishes in the Coastal Plain were less affected by urban land use than in the Piedmont. A smaller but still sizable proportion of species (14 out of 31 when abundance weighted) were negatively associated with the urban cover gradient (Table 5, Fig. 13). The distribution of Coastal Plain T_{95} values was relatively uniform between 12-60% (Fig. 13). A number of fishes were found to be acutely sensitive, including the margined madtom (*Noturus insignis*), redfin pickerel (*Esox americanus*), least brook lamprey (*Lampetra aepyptera*), and pirate perch (*Aphredoderus sayanus*). Several species were collected more frequently and/or were more abundant in urban watersheds, including the mummichog (*Fundulus heteroclitus*), satinfin shiner (*Notropis analostanus*), creek chub (*Semotilus atromaculatus*), and the non-native green sunfish (*Lepomis cyanellus*- Fig. 12c).

For species collected in both the Coastal Plain and Piedmont, a greater sensitivity to urban gradients was observed in the Piedmont, almost without exception (Table 6). In some cases, such as the brown bullhead (*Ameiurus nebulosus*), both presence/absence and abundance analyses suggested sensitivity in the Piedmont while neither analysis did in the Coastal Plain. Not only was sensitivity greater in the Piedmont, but species disappeared more rapidly across the urban land use gradient (Fig. 13).

Table 5. Regional summaries of tested fish species responses by count and percent of regional tested species pool (provided in parentheses) to land cover gradients delineated by region.

			Presence/Absence			Abundance		
Land cover	Region	n species	Negative	Neutral	Positive	Negative	Neutral	Positive
Urbanization								
	Coastal Plain	31	8 (25.8)	19 (61.3)	4 (12.9)	14 (45.2)	10 (32.2)	7 (22.6)
	Piedmont	36	20 (55.6)	16 (44.4)	0 (0.0)	26 (72.2)	10 (17.8)	0 (0.0)
Impervious surfaces								
	Coastal Plain	31	9 (29.0)	18 (58.1)	4 (12.9)	16 (51.6)	12 (38.7)	3 (9.7)
	Piedmont	36	18 (50.0)	18 (50.0)	0 (0)	23 (63.9)	13 (36.1)	0 (0)
Agriculture								
	Coastal Plain	36	7 (19.4)	27 (75.0)	2 (5.6)	12 (33.3)	19 (52.8)	5 (13.9)
	Piedmont	38	1 (2.7)	37 (94.6)	1 (2.7)	7 (18.4)	24 (63.2)	7 (18.4)
	Highlands	25	5 (20.0)	18 (72.0)	2 (8.0)	11 (44.0)	12 (48.0)	2 (8.0)

Table 6. Comparison of T_{95} values with respect to urbanization by fish common to both the Piedmont and Coastal Plain physiographic provinces. Only fish that were found to be sensitive to urbanization in at least one province are listed. Bold values indicate greater sensitivity; if curves were not divergent the value is listed as non-significant (n.s.).

	Presence/absence		Abundance	
Species	Coastal Plain	Piedmont	Coastal Plain	Piedmont
Ameiurus natalis	n.s.	n.s.	n.s.	**48.1**
Ameiurus nebulosus	n.s.	**48.1**	n.s.	**45.5**
Clinostomus funduloides	n.s.	n.s.	59.8	**33.0**
Etheostoma olmstedi	n.s.	**51.3**	n.s.	**43.3**
Lepomis gibbosus	n.s.	n.s.	n.s.	**48.1**
Luxilus cornutus	n.s.	**45.2**	59.3	**20.3**
Notropis hudsonius	n.s.	**48.1**	n.s.	**37.6**
Notemigonus crysoleucas	n.s.	n.s.	**36.2**	45.5
Noturus insignis	**41.1**	43.4	34.8	**22.6**
Petromyzon marinus	n.s.	**53.8**	n.s.	**45.6**
Semotilus corporalis	51.5	**48.1**	48.0	**38.4**

As expected, responses of fish to ISC gradients were very similar to those observed along the urbanization gradient except that responses occurred at much lower levels of ISC. T_{95} values for ISC-sensitive fishes ranged from 1.8-20.5%, corresponding D_1 valueswere between 0.3 and 14.1%. Most fishes sensitive to urbanization were sensitive to ISC. As with urbanization, some species were more common (redbreast sunfish, *Lepomis auritis* and swallowtail shiner, *Notropis procne*), in greater abundance (green sunfish), or both more common and abundant (mummichog and satinfin shiner, *Notropis procne*) in Coastal Plain watersheds with high ISC.

Agriculture

Though overall the effects of the agricultural land cover gradient were reduced relative to responses to the urban gradient, a number of species were affected, both positively and negatively. The effects from agriculture varied among regions and species.

Among regions, Highland ichthyofaunal distributions were the most affected by agriculture. Nearly half (44%) of species tested in the Highlands were found in lower abundances as agriculture increased, while 20% were found to be reduced when comparing presence/absence curves (Table 5). All tested species of salmonids and cottids were negatively affected by agriculture. Three species were positively associated along the agricultural gradient: the central stoneroller (*Campostoma anomalum*), common shiner (*Luxilus cornutus*) and largemouth bass (*Micropterus salmoides*).

In contrast to the Highlands, fish distributions in the Coastal Plain and especially the Piedmont were less affected by agriculture. In these regions, no more than one-third of species were negatively associated (presence/absence or abundance) with agriculture, and in the Piedmont the number of species that were positively associated matched the number of negatively affected species (Table 5). Interestingly, a number of species that were found to be reduced in Highlands agricultural watersheds were insensitive to the same land use in Piedmont streams, including the Blue Ridge sculpin (*Cottus caeruleomentum*) and brook trout (collected with apparently no reduced abundance in watersheds with 98 and 100% agricultural cover, respectively).

Sensitivity analyses

Land use sensitivity values appear to be unaffected by species rarity. For four out of five tests (all regressions of T_{95} values for agriculture and for urbanization in the Piedmont), no significant relationship was apparent (F-value range=0.03-3.04, p-value range=0.1119-0.8755). The exception was the relationship between Coastal Plain urbanization abundance-T_{95} values and species collection frequency (F-value range=4.89, p-value range=0.0471, r^2=0.23); however, the relationship was negative.

The Monte Carlo randomization analyses suggest that the CFD approach was robust when determining whether or not a species is deemed landscape stressor-sensitive. For each of the five tested species, the statistical outcome was homogeneous between the calculations derived from the Monte Carlo procedure and entire expected dataset.

Greatest Conservation Need Fishes

Responses of GCN fishes to land cover varied considerably by land use class and species (Table 7). Urbanization negatively affected 7 out of 8 GCN species. However, some GCN species, such as the rosyside dace and silverjaw minnow (*Notropis buccatus*), were moderately tolerant to urbanization, responding negatively only with abundance and possessing high T_{95} values (60% for the silverjaw minnow). Agriculture affected proportionally fewer GCN species than urbanization (two exhibited positive associations). Several species without GCN status were more sensitive to urbanization than nearly all GCN fishes; these included the pirate perch, redfin pickerel, river chub, and rosyface shiner.

Forecasted change in the Middle Patuxent River

Urban expansion between 2001 and 2030 will likely induce substantial decline in the distribution and abundance of fallfish in the Middle Patuxent River (Fig. 14). In 2001, fallfish potentially inhabited the entire watershed, including seven first-order tributaries where urban cover fell below the D_1 value. By 2030, fallfish will likely be extirpated from the lower Middle Patuxent mainstem, Cricket Creek, and portions of two tributaries in the north of the watershed. Only one first-order tributary lacking urban-associated risk of population decline will remain classified as such.

Portions of the Middle Patuxent River are projected to lose substantial representative ichthyofaunal diversity due to urbanization by 2030 (Fig. 15). All richness estimates include the 11 urban-tolerant species. Least sensitive estimates (based on presence/absence T_{95} values) predict a subwatershed average species richness decline of 12% and a maximum of 50%. Under most sensitive estimates (using D_1 values), average and maximum species richness loss is 26% and 45%, respectively. The slightly lower maximum estimate under the most-sensitive scenario occurs because the 2001 species pool is relatively smaller than in the least-sensitive scenario. Average loss of sensitive species richness in most- and least-sensitive assessments is 28 and 91%, respectively. Projected richness decline is spatially heterogeneous. For instance, fish biodiversity is most likely to decline in the lower

mainstem and Cricket Creek, while upper mainstem reaches and some tributaries (particularly in the west) may retain many sensitive species. **Discussion**

Distinct patterns of fish species responses to land use exist among contiguous regions in Maryland. For example, Piedmont ichthyofauna are acutely vulnerable to urbanization:

Table 7. Summary of responses to land use for fishes designated as greatest conservation need (GCN) and those deemed most vulnerable by our analysis (Abundance T_{95} values <20 for urbanization or agriculture) that currently lack GCN status in Maryland. Species are deemed GCN by Kazyak (2005) except *Anguilla rostrata*, included due to widespread decline (Haro et al., 2000). Species not tested for responses to urbanization are filled grey, those not found to be significantly different than expected are listed as not significant (n.s.), positive responses are noted with a plus sign (+).

Classification	Species	Region	Urbanization T_{95}		Agriculture T_{95}	
			P/A	Abun	P/A	Abun
GCN	*Acantharchus pomotis*	CP			75.5	72.0
	Anguilla rostrata	CP	n.s.	n.s.	n.s.	n.s.
		Pied	n.s.	n.s.	n.s.	n.s.
	Clinostomus funduloides	CP	n.s.	59.8	n.s.	n.s.
		Pied	n.s.	33.0	n.s.	n.s.
	Enneacanthus gloriosus	CP	49.3	37.0	n.s.	72.0
	Enneacanthus obesus	CP			72.0	66.7
	Etheostoma blennioides	Pied	43.4	29.7	n.s.	+
		H			n.s.	65.1
	Etheostoma fusiforme	CP			74.1	72.0
	Hypentelium nigricans	Pied	43.4	37.6	n.s.	n.s.
	Lampetra aepyptera	CP	42.2	22.7	n.s.	n.s.
	Lepomis gulosus	CP			55.9	40.4
	Notropis buccatus	Pied	n.s.	60.5	n.s.	+
	Salvelinus fontinalis	Pied	13.2	12.1	n.s.	n.s.
		H			34.8	22.5
Most vulnerable w/o GCN status	*Aphredoderus sayanus*	CP	13.8	12.0	n.s.	n.s.
	Esox americanus	CP	41.7	16.1	n.s.	n.s.
	Nocomis micropogon	Pied	20.3	15.2	n.s.	n.s.

Notropis hudsonius	CP	n.s.	n.s.	n.s.	19.4
	Pied	48.1	37.6	n.s.	+
Notropis rubellus	Pied	8.5	7.3	n.s.	74.9

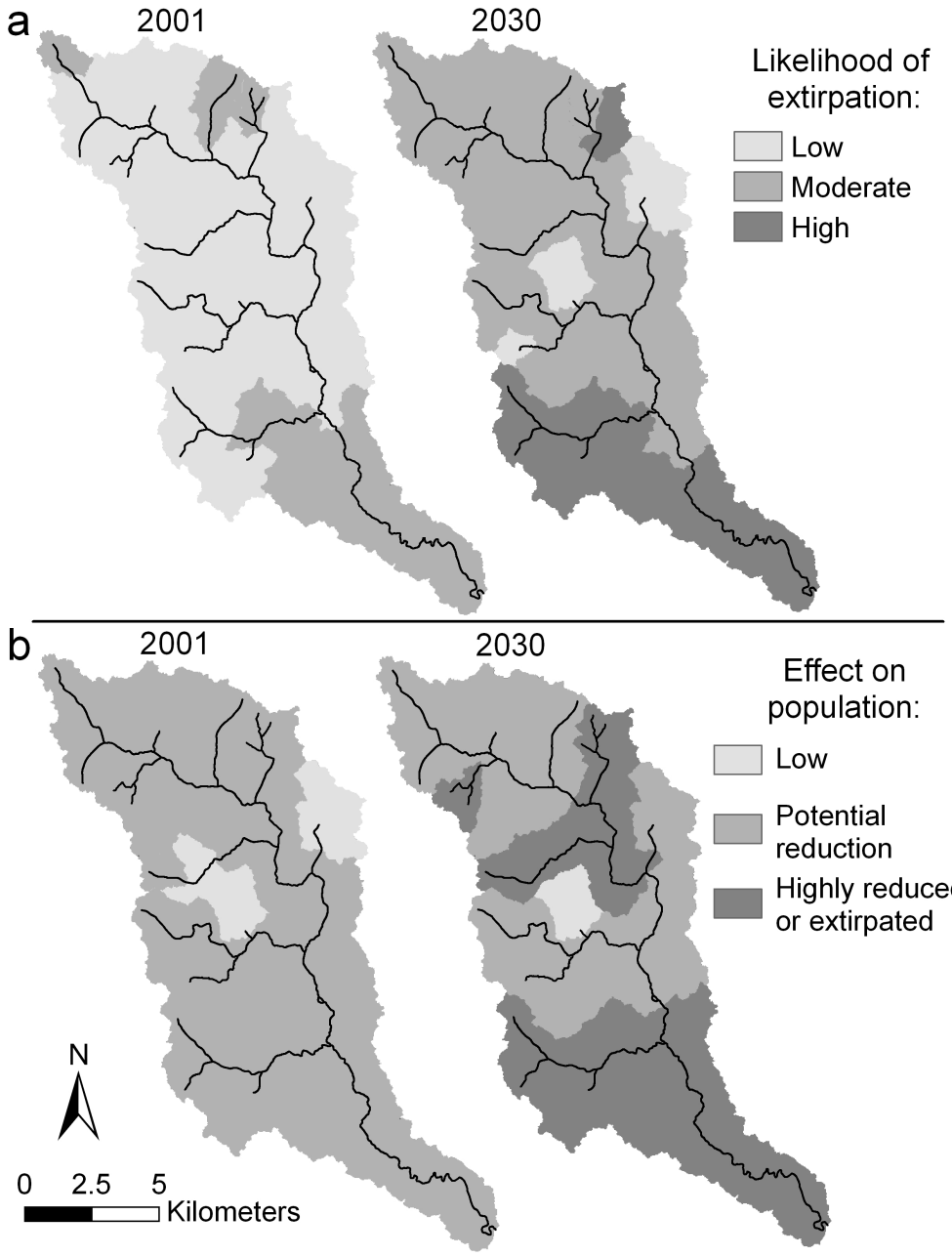

Figure 14. Effect of urban development between 2001 and 2030 on fallfish (*Semotilus corporalis*) (a) distribution and (b) abundance in the Middle Patuxent River watershed. Extirpation and population reduction likelihood were based on presence/absence and abundance assessments, respectively. Extirpation or population

reduction risk was considered low if a reach was urbanized less than the fallfish D_1 value, moderate if between the D_1 and T_{95}, and high if greater than the T_{95}.

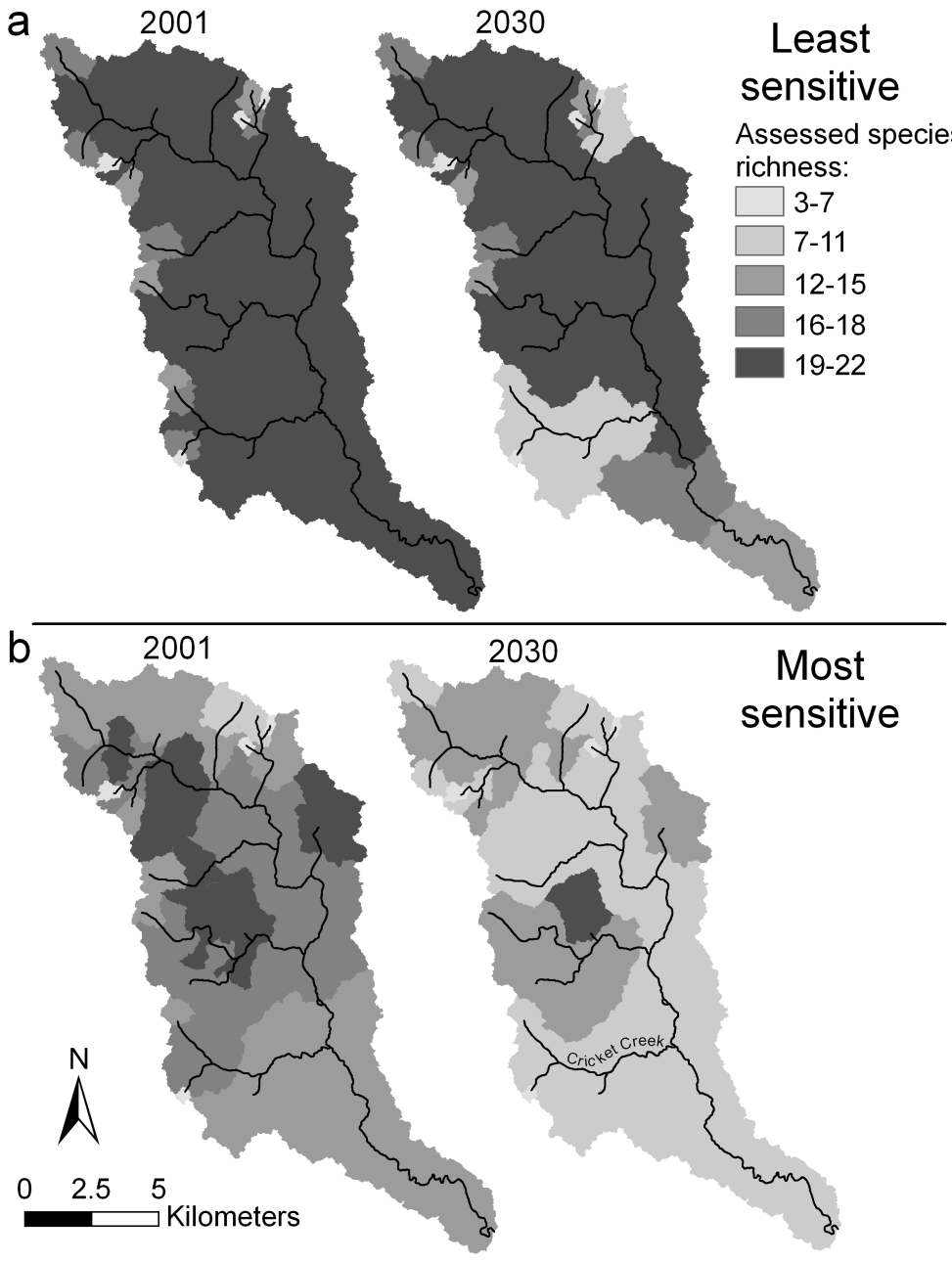

Figure 15. Effect of urban development between 2001 and 2030 on species richness (those tested for landscape stressor sensitivity) in the Middle Patuxent River watershed based on presence/absence D_1 and T_{95} values for each species. Least sensitive estimates (a) assume a fish is present if the level of subwatershed urbanization was then less species T_{95} values. Most sensitive estimates (b) include fish species only when subwatershed urbanization fell below D_1 values for each species.

nearly three-fourths of tested species respond negatively. In contrast, though a sizable proportion of Coastal Plain fishes are urbanization-sensitive, more fishes in this region exhibit a neutral response and some even show a positive response to ISC and urban cover. Regional disparities in sensitivity to land use also frequently occur at the species scale. For instance, the brook trout is the most agriculture-intolerant species in the Highlands but exhibits no apparent sensitivity to agriculture in the Piedmont; however, it is sensitive to impervious surfaces across the state of Maryland (Stranko et al., 2008). Furthermore, 9 out of 11 urbanization-intolerant species shared between the Piedmont and Coastal Plain exhibited greater sensitivity in the Piedmont, adding weight to the assertion that the biotic integrity in Piedmont streams is acutely vulnerable to urban development.

Studies exploring fish community responses to land use offer conflicting evidence for regionally distinct response patterns. Meador et al. (2005) compared stream fish community change along urban gradients in Boston and Birmingham area streams. Some metrics (such as loss of endemic or fluvial species) exhibited region-specific patterns, but the rate of decline in species richness was similar between regions though species composition was dissimilar. Conversely, using indices of biotic integrity developed separately for Maryland Coastal Plain and Piedmont fishes, Morgan and Cushman (2005) reported regional differences in biotic degradation along urban gradients that correspond with our findings. The disparity was partially attributed to a lack of congruency between indices. Our results (Fig. 13, Table 6),

however, suggest that substantial differences in fish sensitivity to urbanization (and other classes of land use) exist among regions, even within a species.

The observed differences may reflect the spatially and temporally complex nature of agricultural and urban land use in Maryland. Agriculture in the Coastal Plain and Piedmont grew rapidly in the early 18th century and dominated the landscape until widespread farmland abandonment started around 1930 (Jacobson and Coleman, 1986; Waisanen and Bliss, 2002; Jackson et al., 2005). As a result, fine sediment deposition in streams remained orders of magnitude above baseline levels for about 200 years and still exerts a legacy in the region's streams (Walter and Merritts, 2008). Agriculture was never as extensive in the Highlands region, though nearly all old-growth forests were lost to logging (Brown et al., 2005). Thus agriculture-sensitive fishes in the Coastal Plain and Piedmont may have been severely reduced in range or extirpated in the past and are not currently present in watersheds where forests have regenerated, as hypothesized in stream biota elsewhere (Harding et al., 1998; Harding, 2003, Wenger et al., 2008).

The mechanisms behind the different sensitivities to urban land use between Coastal Plain and Piedmont streams remain unclear. Streams between these geomorphically distinct regions may vary in rates of physicochemical change as watersheds urbanize. For example, flood flow magnitudes increase more in Coastal Plain urban streams relative to those in the Piedmont, yet Piedmont streams experience substantially higher absolute flood magnitude floods (Moglen et al., 2006). Alternatively, the inherent physicochemical and geomorphic differences between the two provinces may buffer biological assemblages from the effects of

urbanization. For instance, low topographic relief and wetland cover in the Coastal Plain may mediate the hydrologic impact of urbanization in moderately urbanized watersheds. Unfortunately, comparative studies on the effects of urbanization between the two regions have not been conducted for the majority of physicochemical attributes. Our findings, along with related efforts using multimetric biotic indices (Morgan and Cushman, 2005; Goetz and Fiske, 2009) and those that compare physicochemical responses among regions, suggest that interregional comparisons of ecological change in urban streams among these and other geoclimatic regions may prove insightful.

As demonstrated in the Middle Patuxent River watershed, our methodology may be used to forecast biodiversity loss with high spatial and biological resolution. Though freshwater fish community change has been forecasted previously at coarse spatial and biological scales (i.e. degree of biotic homogenization; Olden et al., 2006), the species-specific quantification of landscape sensitivity provided in the response catalog permits detailed prediction of change. The projected decline in species richness in the Middle Patuxent highlights the need for such efforts; despite the conservative (lacking commercial/industrial and transportation) estimates of urban growth used for forecasting, a substantial, but spatially heterogeneous, loss of biodiversity can be expected as a result of urban encroachment. Other means of biological degradation such as habitat fragmentation may also be deduced from such efforts. For instance, the high likelihood of extirpation in the lower mainstem reaches suggest that Middle Patuxent fallfish populations will likely become isolated from other Patuxent River populations by 2030. Though our results allow for such

forecasting only within the ecoregions of the Mid-Atlantic United States, the methodology allows for creation of additional stressor response assessments in other regions and/or assemblages.

Furthermore, the response catalog can be used to assess the effectiveness of GCN status in highlighting those species most vulnerable to land use change. While all tested Maryland GCN fishes were found to be urbanization-sensitive, species such as the rosyside dace and silverjaw minnow are only moderately so (Table 7) and likely respond to a different suite of stressors. In contrast, acutely sensitive fishes without GCN status, such as the river chub, fallfish and rosyface shiner, may experience widespread distributional decline with encroaching urbanization. Therefore a number of currently common species (those listed as most vulnerable without GCN status in Table 7) may require conservation efforts due to urban encroachment in the future. Considering that only 22% of freshwater flora and fauna (fishes, odonates, amphibians, crabs, and plants) globally have been assessed for conservation status (Darwall et al., 2009) and that our technique was capable of identifying highly sensitive species not classified as GCN, application of our methodology may prove valuable as a first step in identifying other species in need of conservation efforts.

Because of the inherent complexity and variation of ecosystem and taxa responses, ecological thresholds should never be treated as static or absolute, but rather as guidelines. A general rule has been that stream fish communities rapidly degrade as watershed ISC exceeds 10-15% (Klein 1979; Wang et al., 2000, 2001). Our results suggest that degradation and biodiversity loss may occur even at the lowest levels of land use conversion, which has been shown for communities

elsewhere (Meador et al., 2005; Moore and Palmer, 2005). In other cases, community-level changes may not be expressed until a sufficient number of taxa are already severely affected and well beyond their species-specific tolerance thresholds (Wang et al., 1997; Roy et al., 2003; King et al., 2005). For Maryland's freshwater fishes, response thresholds appear to be region-dependent and probably also depend on site-specific characteristics such as the configuration of land use within watersheds, and/or potential interactive effects of multiple landscape stressors (Sponseller et al., 2001; Booth, 2005; King et al., 2005). Such attributes further enforce the idea of fuzzy thresholds, and allowing development up to an absolute value may endanger many populations. However, our results can be used to assess the relative vulnerabilities among species, regions and classes of land use, as well as providing guidance on strategies to prevent fish biodiversity loss. Regardless of uncertainties associated with the D_1 and T_{95} values, our approach appears to be robust when identifying which taxa exhibit positive or negative responses to landscape stressors.

Landscape-scale analyses may have limitations due to their large spatial extent. At large scales, land use classes may not be independent of one another, and more than one may simultaneously affect stream ecosystems (King et al., 2005). In our dataset, urban and agricultural uses were more negatively correlated with one another relative to natural cover in the Piedmont and Coastal Plain while urban watersheds were rare in the Highlands (Utz et al., 2009). Potential stressors may also interact (Woodward et al., 2002; Merovich and Petty, 2007) and make interpretations difficult even in large datasets. Our approach did not directly consider the full suite of land-use

induced physicochemical stressors and interactions that simultaneously affect lotic organisms, but that was not our objective. Rather than quantify the amount of variance explained by each stressor, we used land uses as surrogates for the many potential stressors to identify the minimum detectable effects of a land use as well as when an organism is expected to disappear. Thus our approach implicitly incorporates additive and/or interactive effects of multiple physicochemical stressors that exist in impacted streams. A final consideration is that our assessment point thresholds (the critical value, D_1 and T_{95}) need not be considered fixed points, because there is uncertainty associated with any analysis; each of these assessment points can be altered to accommodate one's comfort with uncertainty.

In summary, we identified highly variable patterns in fish distributions along land use gradients both within and among species and regions. Piedmont fishes appear to be considerably more vulnerable to urbanization relative to those of the Coastal Plain, while Highland fishes are most affected by agricultural land use. The regional trends may partly result from different land use history, but also suggest dissimilar rates of physicochemical change with land conversion among regions. Several species show increased sensitivity to land use when samples are abundance-weighted, implying that further reductions in distributions from existing urban and agricultural development may be imminent. Additionally, species both with and without current conservation priority status may experience substantial reductions in distributions if current trends in land use change continue. In light of the increasing human population growth and land conversion in the mid-Atlantic region, our results cataloging regional land use

sensitivity of fishes should prove useful for establishing conservation priorities and planning future development to help minimize biodiversity loss.

CHAPTER IV

INTER- AND INTRA-REGIONAL VARIABILITY IN COMMUNITY-SCALE RESILIENCE TO URBANIZATION

Both natural and human induced landscape-scale environmental attributes shape the composition of biotic communities in streams. Hydrogeomorphic properties that vary among landscapes such as topographic relief, geologic setting and soil regime directly influence the physicochemical and hydrologic framework of stream flow. Because hydrology and physicochemistry structures aquatic habitat, community composition typically varies among streams in different geoclimatic settings (Poff and Ward 1989, Johnson 2000, Mykra et al. 2004). Human activity on the landscape may also exert strong influence on lotic community composition. Processes such as agricultural development, urbanization and deforestation lead to substantial physicochemical and hydrologic adjustment in streams, which induces community-scale adjustment and biodiversity loss (Richter et al. 1997, Allan 2004).

One understudied but potentially informative facet of landscape-scale stream ecology involves the interactive dynamics of natural and anthropogenic attributes. Recent work has shown that hydrologic and chemical shifts along urban and agricultural land use gradients may vary among regions (Liu et al. 2000, Poff et al. 2006, Sprague and Nowell 2008). Such variability in abiotic impact along identical stressor gradients could allude to disparities in the extent of biotic degradation among geoclimatic regions. Interregional comparisons of index of biotic integrity (IBI) decline along gradients of agricultural and urban development suggest that this may be the case (Kennan 1999, Morgan and Cushman 2005, Barker et al. 2006). Despite

explicit calls for further examination of land use-physiography interactions in stream ecology (Karr and Chu 2000, Walsh et al. 2005, Poff et al. 2006), few have directly addressed the phenomenon.

Although urbanization in particular induces severe stream ecosystem degradation, the potential for interregionally variable impact on biotic communities exists. Impervious surface cover (ISC; rooftops and pavement) associated with urban growth promotes frequent and intense flood events, which are often determined to be the most significant (though not sole) driver of biodiversity loss in urban streams (Roy et al. 2005, 2006, Degasperi 2009). While such a pattern is generally consistent (Paul and Meyer 2001, Walsh et al. 2005), nuances in the relationship associated with interregional- or local-scale factors have been detected. For instance, Utz et al. (2009) detected greater sensitivity of benthic macroinvertebrate taxa to ISC in the Piedmont physiographic province of eastern North America relative to the adjacent Coastal Plain. On a smaller spatial scale Snyder et al. (2003) concluded that steep channel slopes heightened the sensitivity of fish communities to urbanization. Both aforementioned studies demonstrate increased tolerance to urbanization in watersheds that naturally attenuate storm flow (for instance those with gentler slopes or a more permeable geologic setting). In light of the rapid urban growth projected to occur in the coming century (Theobald et al. 2009), a descriptive framework of inter- and intraregional stream sensitivity to urbanization could be crucial for effective management and conservation.

Identifying interregional and intraregional differences in community tolerance to land use change requires careful consideration of the biotic response that is modeled.

IBI systems typically consist of ecoregion-specific metric criteria (Stribling et al. 1998), rendering interregional comparisons of relationships inappropriate. Further, IBI scoring applied to a large population of streams ignores the inherent variability of biotic communities across stream forms and over time. An increasingly used alternative involves RIVPACS (River InVertebrate Prediction And Classification Scheme), which models the ratio of observed taxa collected at a site compared to the number expected (Hawkins et al. 2000). However, RIVPACS neglects the fluctuating total and relative abundances of organisms which may indicate biotic integrity or response to a stressor. An ideal means of quantifying intra and interregional community sensitivity to land use change would inherently acknowledge the natural variability of communities both through time and among stream forms.

Given the increasingly alarming status of freshwater invertebrates worldwide (Strayer 2006) and rapid urban growth in the Mid-Atlantic region (Brown et al. 2005), I sought to the quantify sensitivity of each distinctly structured stream macroinvertebrate community to ISC in the two physiographic provinces of Maryland where urban growth is most extensive. I used least-impacted sites from a large dataset (the Maryland Biological Stream Survey; MBSS) to parsimoniously determine the taxonomic structure of naturally occurring macroinvertebrate communities. The probability of encountering each community along an ISC gradient in impacted sites was then calculated to quantify sensitivity. The impact of agriculture was also tested to determine the potential for that landscape stressor to negatively impact biota. Finally, comparisons of abiotic variables associated with each community were made to determine which, if any, promoted tolerance to ISC. Emphasis on the latter

component was placed on variables that affect stormwater retention (i.e. channel slope, wetland cover and soil permeability).

Methods

Study Region

Benthic invertebrate community sensitivity to ISC was investigated in the eastern Piedmont and Coastal Plain physiographic provinces of Maryland, U.S.A. (Fig. 16). Characteristic hydrogeomorphology varies substantially between the two provinces. Coastal Plain basement rocks are buried by a wedge of unconsolidated sediments ten to hundreds of meters deep (Ator et al. 2005). As a result, Coastal Plain benthic sediments consist of a heterogeneous mix of siliclastic cobble, gravel, sand, silt and clay. Headwater Coastal Plain stream reaches may be <1m wide, possess moderate slopes and relatively large sediment regimes. Downstream reaches are sinuous with primarily fine benthic particles. Maximum channel elevations within the Coastal Plain range from 40 m (on the Eastern Shore) to about 70 m with most topographic relief occurring near incised channels. In contrast, Piedmont gneiss-schist basement rocks are overlain by thin (≤2 m) layer of soil (Swain et al. 2004). Channel gradients in Piedmont streams are typically more than twice as steep compared to those of the Coastal Plain (means of 1.2% and 0.5%, respectively, for MBSS sites) and maximum Piedmont channel elevations exceed 250 m. Piedmont benthic sediments are dominated by boulder, cobble and gravel with occasional bedrock outcrops; mean (watershed size-corrected) channel water depths in Piedmont streams tend to be about 25% shallower. In both provinces, upstream forested reaches are almost entirely shaded during the growing season while further downstream (2^{nd}-3^{rd} order) channels

are at least partially exposed to direct sunlight. Mean Coastal Plain stream temperatures are about 2ºC warmer than in the mostly cool- to coldwater Piedmont streams, potentially due to slight climatic differences between regions.

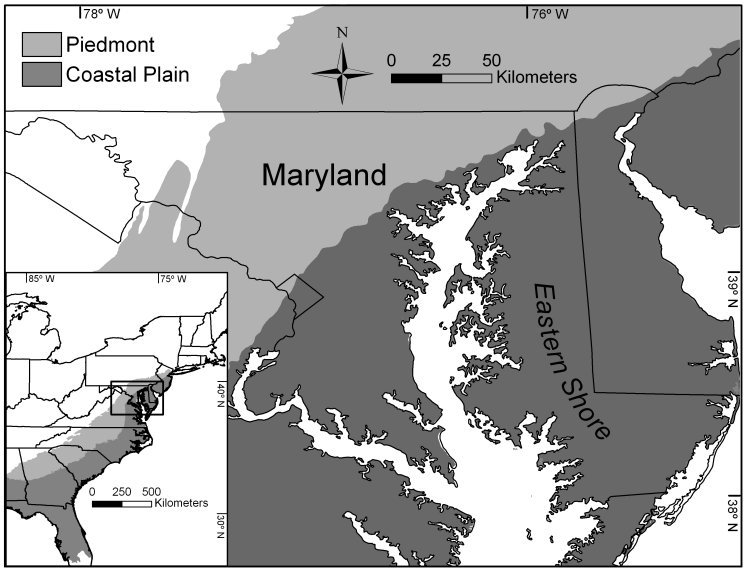

Figure 16. Map of the eastern United States and the state of Maryland with the extent of the Coastal Plain and Piedmont physiographic provinces shown.

Past and present land use regimes are relatively homogeneous between the two provinces. The major metropolitan regions of Maryland (Baltimore and Washington, D.C.) are located on the Coastal Plain-Piedmont boundary. As a result, the intensity of urban development between provinces is similar though concentrated in the easternmost Piedmont and westernmost Coastal Plain. Agricultural land use dominated both provinces until the mid 19th century when large-scale forest regeneration commenced (Waisanen and Bliss 2002, Jackson et al. 2005). Forest and wetland cover is currently more extensive in the Coastal Plain, with agricultural land use relatively more prevalent in the Piedmont. However, the distribution of land use classes in catchments sampled by the MBSS program between the two provinces is broadly similar (Utz et al. 2009).

Biological data

Invertebrate data were derived from rounds I (1995-1997) and II (2000-2004) of the MBSS program. The dataset consists of 1,738 Coastal Plain and Piedmont stream macroinvertebrate collections from 1,361 randomly selected reaches (254 sites were sampled more than once). Samples were collected in the spring (March 1-April 30) by physically disturbing 1.88 m^2 (20 ft^2) of representative benthic habitat upstream of a D-net. Chemical and habitat variables were quantified at the time of macroinvertebrate sampling as well. A 100-individual subsample of each collection was identified to genus except Oligocheate worms, which were identified to family. The identified subsamples were used to quantify macroinvertebrate communities.

Geographic data

Land use and soil characteristics were quantified at the watershed and riparian scale for each MBBS site. Watershed boundaries were delineated using a 30 m resolution elevation dataset (U.S. Geological Survey). Land use data were derived from the 2001 National Land Cover Database (USEPA 2008), which included estimates of ISC. Percent Anderson-1 level (i.e. urban, agriculture, wetland) land use and ISC were calculated at two scales: 1) the entire watershed and 2) within a 200m riparian buffer zone on both sides of the channel network upstream of each site (Fig. 17). Soil watershed attributes were extracted from the State Soil Geographic (STATSGO) spatial database (NRCS 2009); variables averaged for each site at the watershed scale included soil thickness, permeability, and percent clay.

Statistical analyses

A number of data filtering and transformation steps were performed before all analyses. Organisms in the family Chironomidae were aggregated into six subfamilies and all abundance data were relativized (by the total number of organisms in the sample identified to genus) and $\log_{10}$-transformed. Taxa collected from <10% of reference reaches (for reference community identification) or all samples (for

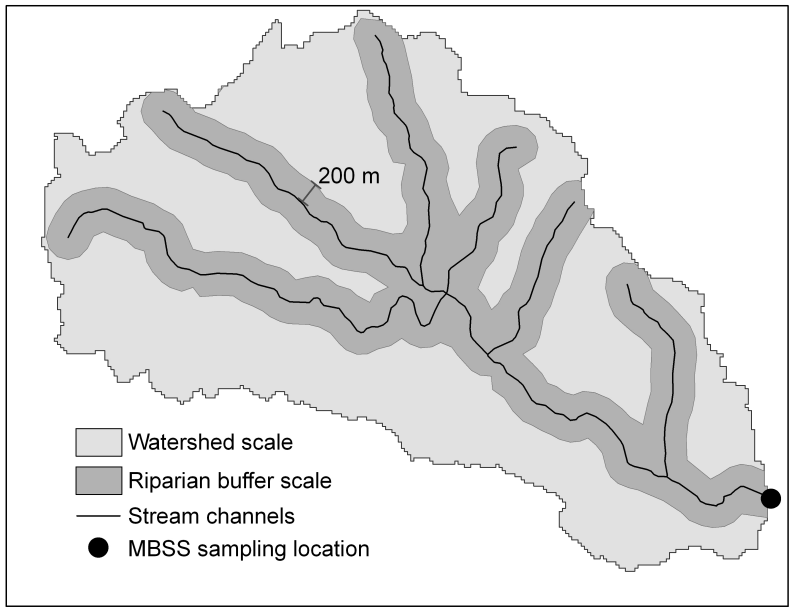

Figure 17. Hypothetical map of an MBSS site watershed depicting the two spatial scales used in quantifying community sensitivity to landscape stressors.

community sensitivity analyses) were deemed to rare and excluded to prevent noise in certain multivariate statistical procedures. Abundance data were averaged across years for analyses regarding reference site community structure for sites sampled more than once. All procedures were performed separately for Coastal Plain and Piedmont streams.

Identifying communities in least-impacted sites and the subsequent analysis of community sensitivity to landscape stressors included a number of integrated statistical analyses. The entire process, described below, is summarized in Fig. 18

Community structure was first assessed via the detection of distinguishable groups in least-impacted (hereafter reference) streams. Sites were deemed in reference condition if each of the following conditions at the watershed-scale were met: <3% urban cover, <1% ISC, and <50% agricultural cover. If a site met the land use conditions but possessed an invertebrate IBI score (Southerland et al. 2007) less than 3.0, it was considered degraded and removed from the reference site pool.

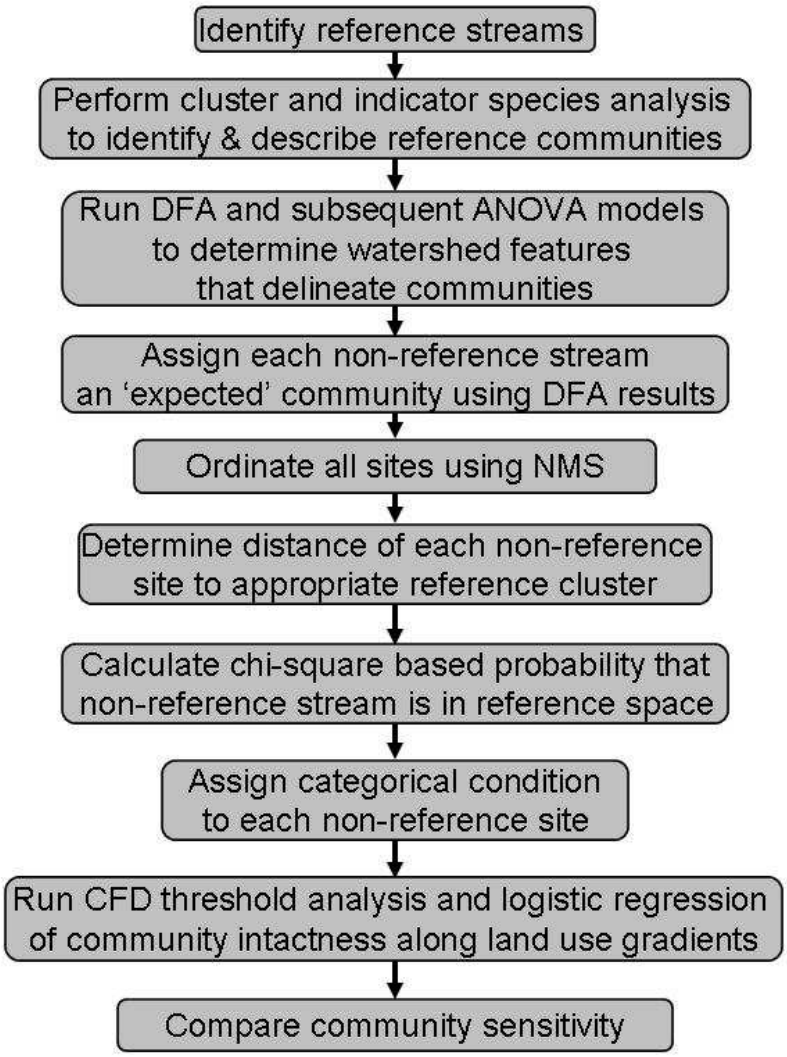

Figure 18. Schematic illustrating statistical procedures used to identify reference communities and assess community sensitivity to landscape stressors.

Hierarchical cluster analyses (flexible beta linkage, β=-0.25) and subsequent indicator species analysis on the cluster scheme (Dufrene and Legendre 1997) were used to identify and describe reference site community composition. Mean p-values and the total number of statistically significant ($p<0.05$) indicator taxa were used as equally weighted criteria in determining the optimal number of clusters (i.e. communities) present in reference sites (McCune and Grace 2002).

Once the optimal community structure scheme was identified, the physicochemical attributes characterizing each group were quantified and non-reference sites were assigned to expected reference communities. Stepwise discriminant function analysis (DFA) was used to determine which physicochemical variables (listed in Table 8) delineated reference groups from one another. Subsequent analysis of variance (ANOVA) and Fishers least significant difference post-hoc comparison tests were performed on statistically significant DFA variables to determine which, if any, differed among reference groups. The DFA system was also used to assign expected reference groups to non-reference sites. If the physicochemical attributes of a non-reference reach were predicted to support a particular reference community at a probability of 0.90 or greater, it was assigned the single reference group. However, non-reference sites were assigned multiple expected communities if the DFA system assigned a probability of membership >0.10. The

multiple expected community option was implemented in recognition of uncertainties in the reference community and DFA classification systems.

Table 8. Physicochemical variables tested for distinguishing reference communities in the discriminant function analyses (DFA).

Variable	Transformation	Source
Watershed size (km^2)	log_{10}	GIS
Elevation (m)	log_{10}	GIS
Slope (%)	log_{10}	MBSS
pH	log_{10}	MBSS
ANC ($\mu eq\ L^{-1}$)	square-root	MBSS
Dissolved organic carbon ($mg\ L^{-1}$)	log_{10}	MBSS
Maximum depth (cm)	square-root	MBSS
Wetland cover (%)	log_{10}	NLCD
Soil thickness (cm)	none	STATSGO
Soil permeability ($cm\ hr^{-1}$)	none	STATSGO
Soil clay composition (%)	none	STATSGO

An ordination system was used to quantify the community-scale similarity of non-reference samples to each reference group. All samples (reference and non-reference) were ordinated in three-dimensional nonmetric multidimensional scaling (NMS) systems based on Bray-Curtis dissimilarity measures. For each cluster of reference group samples, a 95% confidence ellipsoid (i.e. reference domain) was calculated in ordination space using the Mahalanobis distances of NMS scores. The probability (from 0 to 1) that a non-reference sample fell within a reference domain was determined by calculating the Mahalanobis distance of the non-reference sample to the corresponding reference confidence ellipse centroid. If the probability exceeded

0.05, it was deemed within the domain; those scoring less than 0.05 were considered outside of the domain. A hypothetical example of the above steps is illustrated in Fig. 19.

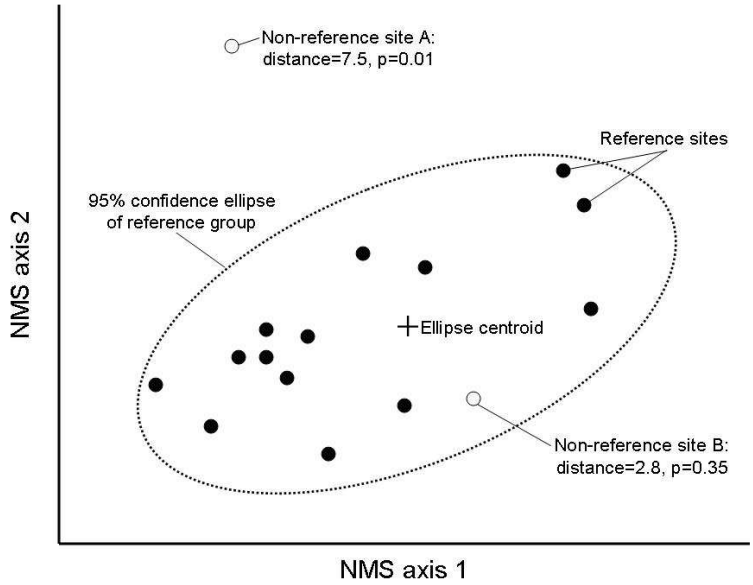

Figure 19. Hypothetical example of 2-dimensional NMS ordination of a reference group and two non-reference sites. Non-reference site A is significantly outside of the reference group confidence ellipse, while site B is not. Mahalanobis distances of non-reference samples (denoted by the word 'distance' in the figure) take into account the elliptical shape of the reference space; thus distances to the centroid do not scale linearly with respect to the two axes.

The probabilities of reference group membership were used to quantify community sensitivity to ISC and agriculture. Cumulative frequency distributions (CFD) along each land cover gradient of samples falling within reference space (the observed CFD) were compared to the CFD of sites expected to possess the reference community (based on the DFA system). The CFD approach is outlined in detail by Utz et al. (2009). Briefly, whether or not the expected and observed CFDs differed significantly was tested using a chi-square goodness of fit test on based on the 90th percentile on the x-axis for the expected CFD (i.e. 10% above and 90% below on the

expected CFD compared to the % above and % below on the observed CFD). If the curves significantly differed, the minimum detectable degree of land cover that caused a reduced frequency of community occurrence was estimated by identifying the point on the x-axis where the curves diverged by more than 2% ISC. The maximum tolerance of the community to the land use gradient was also estimated; this was quantified as the degree of the landscape stressor that corresponded to the 95^{th} percentile on the y-axis of the observed CFD. To account for uncertainty in the approach, the procedure was performed for 1000 iterations on randomly-selected sets of expected sites consisting of 80% of the original pool. The proportion of chi-square p-values that were below α=0.05 was calculated and if that proportion fell below 0.05, the community was deemed sensitive to the land cover gradient. Further, the mean minimum detection of impact from the permutation procedure was calculated to assess community sensitivity. Both gradients of ISC and agriculture (watershed- and riparian-scale) were analyzed.

Reference community sensitivity to ISC and agriculture was also quantified using logistic regression. Logit models were calculated to determine if there was congruence in the results relative to the novel CFD technique. The probability that a sample fell within a reference domain for those sites expected to possess the community (based on the DFA system) was modeled along both spatial scales of ISC and agriculture for each group.

Community sensitivity to ISC was compared among all reference groups with respect to hydrogeomorphic variables that influence storm water retention on the landscape. ISC sensitivity was ranked via maximum tolerance values derived from

the CFD approach. Mean (log_{10}-transformed) slope, percent wetland cover, and (untransformed) soil permeability was compared among groups of reference sites using ANOVA models and Fisher's least significant difference post-hoc tests.

Results

Community structure and influence of physicochemistry

Reference streams in both provinces supported distinct communities that were significantly associated with physicochemical variables. Cluster and indicator species analyses suggested that Piedmont and Coastal Plain reference streams sustained two and three taxonomically discrete communities, respectively (hereafter denoted as groups A-E). The number of significant indicator taxa ($p<0.05$) that delineated groups ranged from two (in Coastal Plain group D) to ten (in Piedmont group B; Table 9). Certain taxa, such as the mayflies *Stenonema* and *Acerpenna*, were significant indicators for reference groups in both provinces. The stepwise DFA procedure identified five significant physicochemical attributes used to discriminate among reference groups in the Piedmont and four in the Coastal Plain (Tables 10 and 11). Watershed size and pH influenced community identity in both provinces. Channel slope, soil clay content and dissolved organic carbon (DOC) were significant delineating parameters in the Piedmont while soil thickness and elevation were significant in the Coastal Plain. Two variables (pH and soil clay content) selected by the stepwise Piedmont DFA as predictors of community identity did not significantly differ between groups (Table 10); the means of all other DFA-selected parameters significantly differed between at least two reference communities (Tables 10 and 11).

Community sensitivity to ISC and agriculture

All reference communities exhibited sensitivity to ISC though variably between and within physiographic provinces. The proportion of chi-square p-values from the CFD permutation procedure that resulted in a p-value above 0.05 was zero with the

Table 9. Statistically significant indicator taxa that delineated Coastal Plain and Piedmont communities. Taxa are ordered by indicator value (largest to smallest).

Community	Taxa
Piedmont	
A	*Ephemerella, Chimarra, Optioservus, Stenonema, Acentrella*
B	*Diplectrona, Neophylax, Baetis, Lype, Pycnopsyche, Isoperla, Anchytarsus, Tallaperla, Eccoptura, Acerpenna*
Coastal Plain	
C	Tanytarsini, *Stenonema, Dubiraphia, Ancyronyx, Simulium, Lype,* Chironomini, *Polycentropus, Pycnopsyche, Cheumatopysche*
D	*Leptophlebia, Leuctra*
E	*Acerpenna, Ephemerella, Neophylax, Oulimnius, Optioservus, Eccoptura, Prosimulium,* Diamesinae, *Probezzia*

exception of Coastal Plain group C along the riparian-scale ISC gradient (2 out of 1000 p-values were over 0.05). Maximum tolerance to ISC ranged from 3 to 14.7% at the watershed scale and 1.2 to 11.1% at the riparian buffer scale (Table 12). The mean minimum detection of impact was consistently low among all communities, with none possessing values over 0.6%. All Coastal Plain communities were less sensitive to those of the Piedmont with respect to maximum tolerance estimates. Communities in the Piedmont exhibited near homogeneous sensitivity to ISC but Coastal Plain groups were variable. The most ISC-tolerant Coastal Plain communities (group C) were characteristic of large, low-elevation streams in watersheds with thin soils,

while the most sensitive (group E) were small, relatively alkaline streams at higher elevations.

In contrast to ISC, nearly all communities exhibited tolerance to agriculture. Among the ten tests (5 communities × 2 gradients) in the CFD approach, nine showed

Table 10. ANOVA results and means of Piedmont reference group physicochemical variables selected by the DFA model. Values shown are untransformed means (±95% confidence intervals); statistical comparisons were performed on log_{10}-transformed values with the exception of soil clay content (which was not transformed).

			Means	
Variable	F	p-value	Group A	Group B
Watershed size (km^2)	15.6	0.0005	1.3 ± 0.7	20.8 ± 11.8
Slope (%)	5.7	0.0244	1.1 ± 0.3	1.8 ± 0.6
DOC (mg/L)	12.2	0.0017	1.7 ± 0.3	0.9 ± 0.2
pH	1.9	0.1754	7.2 ± 0.2	7.0 ± 0.4
Soil clay content (%)	0.0	0.9300	21.4 ± 1.4	21.1 ± 3.7

Table 11. ANOVA results and means of Coastal Plain reference group physicochemical variables selected by the DFA model. Values shown are untransformed means (±95% confidence intervals); statistical comparisons were performed on log_{10}-transformed values with the exception of soil thickness (which was not transformed).

			Means		
Variable	F	p-value	Group C	Group D	Group E
Watershed size (km^2)	11.7	0.0002	69.4^{A} ± 40.5	9.7^{B} ± 11.2	6.7^{B} ± 9.3
Soil thickness (m)	8.6	0.0010	1.7^{A} ± 0.1	1.8^{B} ± 0.1	1.9^{C} ± 0.1
Elevation (m)	5.4	0.0095	8.0^{A} ± 1.8	19.4^{B} ± 8.7	21.8^{B} ± 12.8
pH	5.0	0.0132	6.4^{A} ± 0.3	6.0^{B} ± .4	6.7^{A} ± .5

no sensitivity to agriculture. Of these, the proportion of chi-square p-values that fell above 0.05 in the permutation procedure ranged from 0.07 to 1. The exception was Piedmont group B to riparian-scale agriculture with a proportion of chi-square p-

values above α=0.05 equal to 0.003. However, Piedmont group B was substantially more tolerant to riparian agriculture relative to ISC; the mean minimum detection of impact was 20.6% and maximum tolerance was 75.5% agricultural cover. Piedmont group B exhibited tolerance of agriculture at the watershed-scale; the proportion of chi-square p-values falling above α=0.05 was 0.986.

Table 12. Reference community sensitivity to ISC (watershed and buffer scales) cover based on cumulative frequency distribution analyses. Each value represents a percentage of ISC.

	Watershed scale		Buffer scale	
Province and group	Minimum detection of impact	Maximum tolerance	Minimum detection of impact	Maximum tolerance
Piedmont				
A	0.1	3.0	0.1	1.3
B	0.1	3.0	0.1	1.2
Coastal Plain				
C	0.2	14.7	0.3	11.1
D	0.1	12.0	0.1	8.8
E	0.6	10.0	0.1	5.5

Logit analyses generally confirmed the results of the CFD approach (Fig. 20). All probability of reference group membership logit functions possessed statistically significant and negative ISC (slope) model terms, with p-values ranging from <0.0001 to 0.0363. Again, Piedmont groups exhibited the greatest (near-uniform) sensitivity to ISC while Coastal Plain streams were consistently more tolerant. Coastal Plain community D was modeled to occur at the highest levels of ISC among all communities, which contrasts the CFD findings (where community C was found to be most tolerant). However, this was partly an artifact of variable intercepts. The

likelihood of a stream supporting community D declined more rapidly along the riparian-buffer scale ISC gradient relative to community C. As in the CFD approach, community E was the most ISC-sensitive of the Coastal Plain groups. Logit analyses along the agriculture gradient also concurred with the CFD results. Of all community occurrence-agriculture tests, only Piedmont group B showed a significant negative relationship to riparian agriculture ($p=0.0217$).

Community sensitivity and hydrogeomorphology

Mean slope, percent wetland cover, and soil permeability varied significantly among reference group sites (Fig. 21). Both mean percent wetland cover and soil permeability increased with each step in rank of tolerance to ISC (based on maximum tolerance values from the CFD analyses). Though sensitivity rank compared to mean slope was relatively more variable, the most tolerant communities were characteristic of streams with the gentlest channel slopes.

Discussion

As expected, macroinvertebrate communities specifically associated with environmental and spatial attributes differed in sensitivity to ISC. Variable tolerance to ISC was detected between and within physiographic provinces, suggesting that both regional and local factors drive divergence in stressor tolerance. Piedmont communities were most vulnerable to the environmental changes induced by ISC: each of the two identified reference groups exhibited near uniform decline in probability of occurrence along the stressor gradient. In contrast, Coastal Plain community tolerance to ISC varied considerably, though each of the three was substantially more tolerant than the two Piedmont communities. Thus streams of the

Piedmont province may require considerably more mitigative action to effectively conserve biotic integrity in watersheds with projected urban development relative to those in the Coastal Plain.

Stream biota appear to be acutely vulnerable to ISC in watersheds that conduct stormwater rapidly to stream channels under natural conditions. Communities associated with watersheds having wetlands, gentler slopes and greater soil permeability were the most tolerant to ISC. Similarly, Snyder et al. (2003) determined that fishes were more vulnerable to urban development in streams with steeper gradients, and Stranko et al. (2008) attributed extensive wetland cover to the retention of brook trout populations in a highly urbanized site. Such findings could result from differing physical disturbance regimes among stream forms. Relatively minor flood events may physically displace macroinvertebrates thereby reducing fitness and increasing mortality in multiple taxa (Gibbins et al. 2007a, b). Steeper slopes, a lack of wetland cover and impermeable soils promote surface runoff during precipitation, which may explain why rural Piedmont streams are subjected to more frequent, short duration, intense flood events relative to those in the Coastal Plain (Utz et al. in review). Further, riparian wetlands (which are more extensive in the Coastal Plain) may mitigate the effects of impervious surfaces on storm flow (Burns et al. 2005). Therefore Coastal Plain biota in moderately urbanized streams may be naturally buffered from the effects of ISC due to the hydrogeomorphic setting.

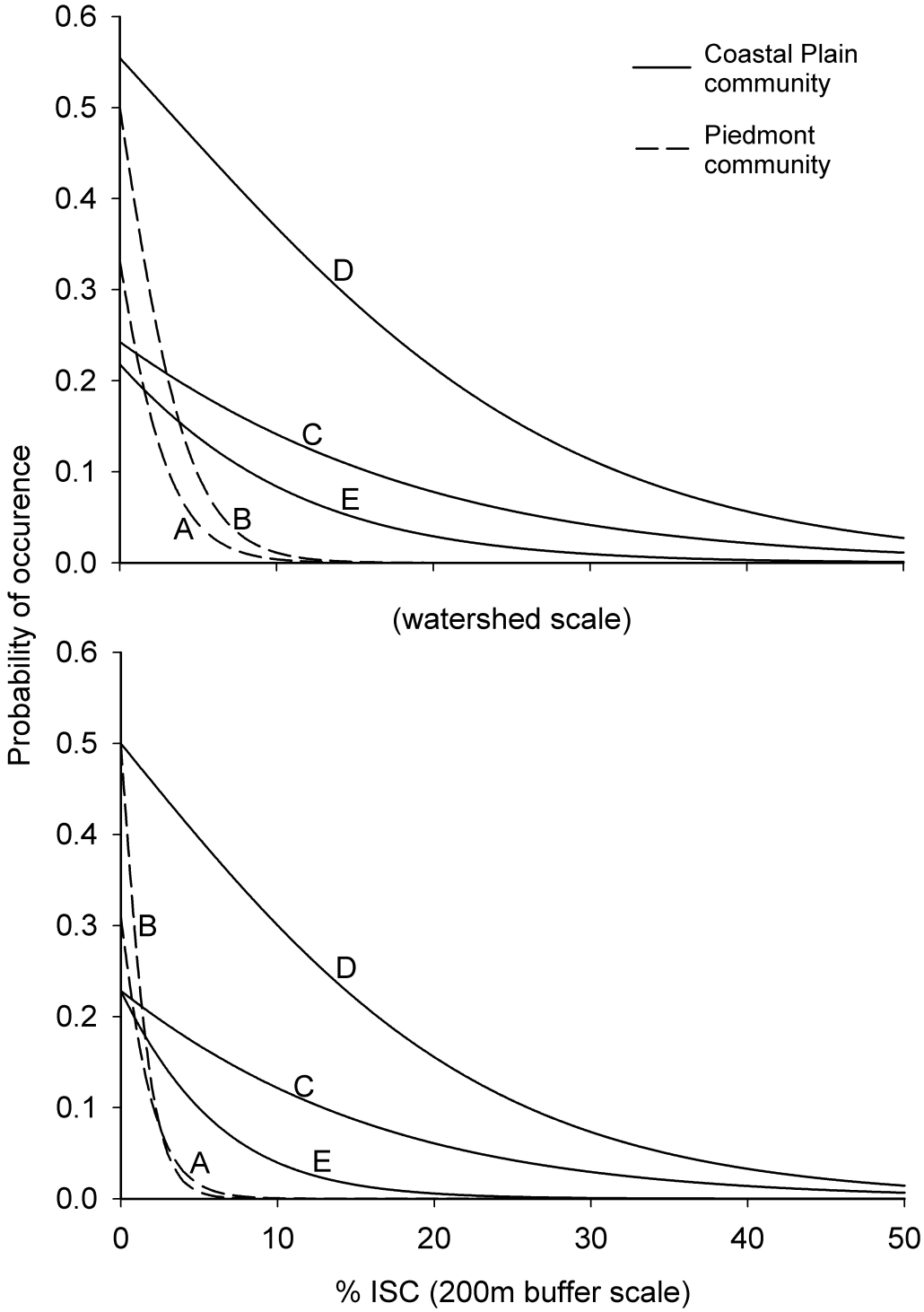

Figure 20. Probability of reference community occurrence logit functions along watershed- and riparian buffer-scale ISC gradients.

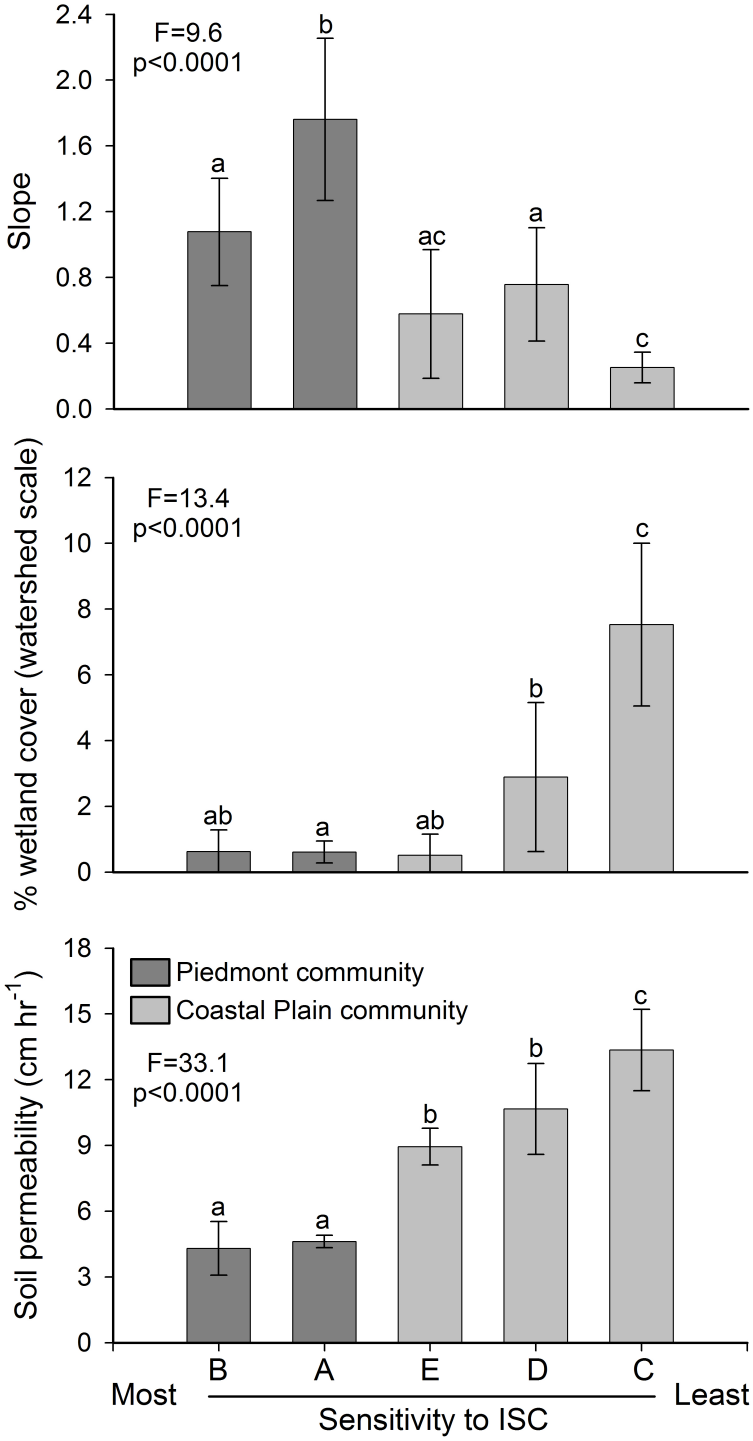

Figure 21. Mean (± 95% confidence intervals) slope, percent wetland cover, and soil permeability among reference streams. Groups are ordered based on ISC with respect to maximum tolerance values derived from the CFD approach.

Contrasting the sensitivity to ISC was the tolerance of each community to agricultural land use. Such findings could have been an artifact of the reference site selection process, as sites with up to 50% agriculture were included in the reference pool. However, such a criterion was necessary, as limiting reference watersheds to those with lower degrees of agricultural cover would have severely reduced the potential suite of sites. Yet biotic communities currently inhabiting Mid-Atlantic streams may possess real tolerance to agriculture. Row crop and pasture cultivation was far more extensive in the study area prior to about 70 years ago, and agricultural practices have induced severe historical geomorphic adjustment in streams (Jacobsen and Coleman 1986, Waisanen and Bliss 2002, Jackson et al. 2005). As a result, many of the agriculture-sensitive organisms may have been extirpated from Maryland streams decades or centuries ago (Harding et al. 1998, Harding 2003). Further, biotic integrity as measured by the presence, abundance and diversity of sensitive organisms shows little impact in highly agricultural Mid-Atlantic watersheds (Moore and Palmer 2005, Utz et al. 2009).

Results suggest that identifying reference assemblages and their associated environmental variables was successful, though some communities may have been overlooked. While many macroinvertebrate genera are widespread and consist of species with variable niches, the life history attributes of some key indicator taxa correspond with the abiotic parameters of streams linked to the delineated communities. For instance, mayflies in the genus *Leptophlebia* inhabit slow-moving waters with abundant detritus likely found in the wetland-rich streams of community

D (Knopp and Cormier 1997, Merritt and Cummins 2008). Similarly, *Oulimnius* beetles prefer interstitial cobble habitat (more likely found in small upland Coastal Plain streams that corresponded with those of community E) while *Dubiraphia* inhabits macrophytes that are more abundant in larger streams (i.e. those of community C; Knopp and Cormier 1997, Merritt and Cummins 2008). Yet the filtering process invoked to create the initial reference site pool may have excluded all representative sites of particular communities endemic to heavily developed regions within Maryland. Such a factor may partially explain why only five communities were identified within the state.

The variable community composition and stressor sensitivity in streams has implications for effective bioassessment. Several related efforts have concurred with my results in concluding that environmental attributes at multiple spatial scales (i.e. among ecoregions and with variables such as watershed size) simultaneously influence stream macroinvertebrate community composition (Sandin and Johnson 2000, Heino et al. 2003, Mykra et al. 2007). While the importance of stratifying bioassessments by ecoregion has long been accepted (Feminella 2000, Gerrittsen et al. 2000, Stoddard 2004), some systems (such as IBI's) may be specifically designed with variable metrics so that sensitivity to a particular stressor is uniform among regions (Astin 2007, Southerland et al. 2007). Yet the heightened sensitivity of Piedmont communities suggests that a regionally disparate response in an IBI score to a land cover gradient (for instance, Morgan and Cushman 2005) represents a potentially ecologically meaningful trend. Acknowledgement of natural community variation in streams within ecoregions has been much more limited. The repeatedly

observed variation in communities along gradients of variables such as stream size (Malmqvist and Hoffsten 2000, Heino et al. 2005, Heino and Paasivirta 2009) likely renders such attributes pertinent when assessing sensitivity to stressors, as the local community composition and environmental setting may both influence the community-scale response to a stressor at a particular site.

Quantifying community sensitivity to landscape stressors among stream forms could also improve the effectiveness of watershed-scale conservation efforts. Though urbanization challenges the conservation of aquatic biodiversity through a substantial suite of abiotic changes, preventative and restorative measures may be implemented to preempt degradation or restore ecosystem health (Palmer and Allan 2006, Roy et al. 2008). Such actions require moderate to substantial financial investment (Hassett et al. 2005). If the retention of biotic communities is a primary management goal in an area with rapidly expanding urbanization, identifying which stream forms support the most vulnerable communities and the natural watershed attributes that promote ISC tolerance could help prioritize resources.

More research to identify specific mechanisms driving the disparate biotic responses among stream forms is necessary. My results support related work (Snyder et al. 2003, Burns et al. 2005, Stranko et al. 2008) in demonstrating tolerance to ISC in watersheds with hydrogeomorphic attributes that promote stormwater retention, and such a conclusion makes intuitive sense as hydrologic disturbance is considered a primary driver of biotic degradation (Roy et al. 2005, 2006, Degasperi 2009). However, my results (as well as the aforementioned studies) were at least somewhat exploratory and were derived from datasets not specifically designed to identify

environmental variables that influence ecosystem sensitivity to ISC. Furthermore, other hydrogeomorphic attributes, such as the contribution of flow derived from groundwater springs (Steffy et al. 2004), may also influence the extent of degradation resulting from ISC. Therefore future comparisons of ecosystem degradation in urban streams should consist of hypotheses that directly address certain hydrogeomorphic and physicochemical properties.

To summarize, community sensitivity to ISC varied among and within physiographic regions and appeared to be influenced by hydrogeomorphic attributes. My findings concur with related efforts as well as those addressing sensitivity to agricultural gradients (Duggan et al. 2004, Barker et al. 2006) in concluding that landscape stressor sensitivity differs among environmental contexts at multiple scales. Biotic sensitivity to ISC appears to be related to hydrogeomorphic variables associated with stormwater retention, such as soil permeability, wetland cover and channel slope. Future efforts comparing impact in urban systems with hypotheses that explicitly consider such factors may contribute to a predictive framework of ISC sensitivity among stream forms. Regardless of the mechanism, biotic communities do not respond homogeneously to landscape stressor gradients and such diversity in sensitivity should be an inherent component of conservation and bioassessment programs.

CHAPTER V

INTERREGIONAL COMPARISONS OF PHYSICOCHEMICAL RESPONSES TO URBANIZATION IN STREAMS

(At the time of dissertation submission, this chapter has been submitted for publication in the journal *Ecological Applications*, titled "Variation in hydrological, chemical and thermal responses to urbanization in streams between two physiographic regions of the Mid-Atlantic United States" by R.M. Utz, K.N. Eshleman, and R.H. Hilderbrand.)

Urban encroachment ranks among the most pervasive drivers of stream ecosystem degradation. Impervious surfaces associated with urbanization route water delivered during precipitation events directly to stream channels that would have otherwise been evapotranspirated or allowed to infiltrate the soil. Moderate to substantial changes in the thermal, chemical, geomorphic, and especially hydrologic regimes of streams ensue, resulting in extensive loss of biodiversity (Paul and Meyer 2001, Walsh et al. 2005). Although the spatial extent of such degradation has traditionally been localized in the vicinity of urban centers, the expansion of exurban growth has exacerbated the scale of risk to aquatic ecosystems. For instance, it has been predicted that approximately 40% of all fifth-order streams within the conterminous United States will be somewhat impacted by urban development by 2030 (Theobald et al. 2009).

A wealth of mostly case study and local-scale efforts has led to a consensus on the general nature of physicochemical change that occurs in streams following watershed urbanization. Repeatedly detected trends in impacted sites among multiple locales have been observed and are now considered central tenets of urban stream ecology. Examples include: heightened spate frequency and magnitude (Konrad et al. 2005,

Roy et al. 2005, Schoonover et al. 2006); elevated temperatures (Wang and Kanehl 2003, Moerke and Lamberti 2006, Nelson and Palmer 2005); increased concentrations and loads of nutrients, metals, dissolved organic carbon and suspended solids (Lenat and Crawford 1994, Groffman et al. 2004, Schiff and Benoit 2007); and geomorphic adjustment such as channel widening and/or incision (Arnold et al. 1982, Pizzuto et al. 2000, Grable and Harden 2006). Each of the aforementioned studies and the majority of related research were typically limited to a single watershed, paired watersheds, or group of sites within a relatively homogeneous geoclimatic region.

Comparing impacts in two or more geoclimatic settings may reveal important discrepancies in the degree of change caused by urbanization, however. Physiographic provinces and/or ecoregions (Omernik 1987) have long been recognized as meaningful spatial templates that demarcate disparities in stream form and function. Such natural variability may convey inherent differences in vulnerability to a landscape stressor. A handful of efforts have explicitly explored the role of physiographic or regional variation on physicochemical change in urban streams. Sprague and Nowell (2008) found that urbanization led to elevated herbicide concentrations in only three of the six urban centers considered. Similarly, Potopava et al. (2005) demonstrated that urban development affected concentrations of total nitrogen and phosphorus differentially among three distinct geoclimatic locations. Poff et al. (2006a) highlighted differences in the degree of correlation between urbanization and multiple hydrologic metrics among four regions of the United States. Despite the insight gained by the above studies and explicit calls for the examination of how physiography may regulate stream ecosystem responses to

urbanization (Walsh et al. 2005), related efforts remain scarce. Yet such work could prove useful for the management of impacted systems: if streams in one geoclimatic setting are acutely vulnerable to change for a given parameter, conservation or restoration efforts could target that parameter over others.

Examining biological impairment (e.g. Karr 1981) represents one means of identifying possible distinct physicochemical responses to urbanization. For instance, between the eastern Piedmont and Coastal Plain physiographic provinces of the Mid-Atlantic United States, loss of biotic integrity along increasing gradients of urbanization appears to be more severe in the Piedmont for both fish (Morgan and Cushman 2005) and macroinvertebrate (Goetz and Fiske 2008, Utz et al. 2009) assemblages. Such consistently observed disparities in biological responses suggest that at least some physicochemical change induced by urbanization may be more severe in the Piedmont province. Although a very large proportion of research on urban stream ecology has been conducted in these regions (Schueler et al. 2009), no direct quantitative comparisons of physicochemical change along urban gradients have been conducted.

Given the discordant nature of biological response to urbanization between the Piedmont and Coastal Plain provinces, we sought to identify any analogous differences in physicochemical degradation. Our goal was not to identify a single parameter that resolved the discrepancy in biological impairment between the two provinces. Rather, we determined which, if any, physicochemical properties were more vulnerable to change in one province relative to the other and quantified divergence when present. We focused on hydrologic, chemical, and thermal

properties of streams commonly affected by urbanization, many of which are considered agents of biological degradation. For each quantified physicochemical parameter, we tested for province-specific differences in rural streams and in the degree of change along a gradient of impervious surface cover (ISC). Analysis of covariance (ANCOVA) was used to construct linear models along ISC gradients; a province term (which compared intercepts) tested for provincial differences in undeveloped streams and an interaction term (which compared regression slopes) determined if the degree of change along the ISC gradient varied between provinces.

Study Area

The eastern Piedmont and Coastal Plain physiographic provinces encompass approximately 197 000 and 423 000 km^2 of land, respectively, in the eastern United States (Fig. 22). Both provinces are characterized by distinct geologic, topographic, and hydrogeomorphic attributes. Gneiss-schist and shale-sandstone crystalline rock

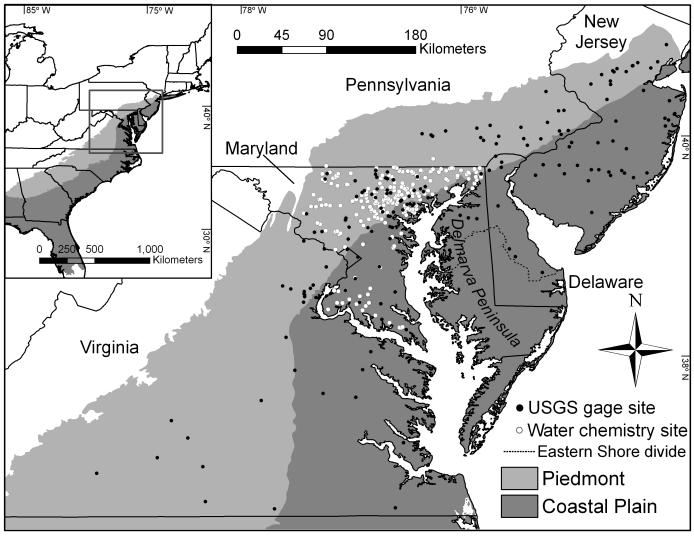

Figure 22. Map of the Coastal Plain and Piedmont physiographic provinces shown at the scales of the eastern United States and Mid Atlantic region. Gage and water chemistry (MDE and Baltimore County) sites are shown; MBSS sites were excluded due to the large sample size.

formations underlay a 1-2 m layer of soil in the Piedmont province (Swain et al. 2004, USDA 2008). The topographic relief of the Piedmont is best described as undulating ridges and valleys that typically range from 15 to 100 m deep; elevation above sea level ranges from 60 to >500 m (Thornbury 1965). Piedmont streams are of steep to moderate gradient and bed sediments consist of boulders, cobble, gravel, and occasional bedrock outcrops. In the Coastal Plain, crystalline basement rock is buried by a wedge of unconsolidated, mostly siliciclastic sediments in depths ranging from <10 m near the Piedmont border (i.e., the "Fall Line") to >3 000 m along the coast of North Carolina (Ator et al. 2005). Uppermost Coastal Plain elevations are 80 to 100 m and topography varies from steeply incised to nearly flat. Streams in the Coastal Plain are of moderate to low gradient and bed sediments are a heterogeneous site-specific mix of cobble, sand, clay and silt.

Data analyses were limited to watersheds within the five state Mid-Atlantic region, an area that includes the northernmost extent of both provinces. Hydrologic data were derived from watersheds throughout the Mid-Atlantic region, while chemical and temperature data were assessed in watersheds exclusively within the state of Maryland. Watershed delineation in the outer reaches of the Delmarva Peninsula is particularly difficult due to low topographic relief and a prevalence of agricultural drainage ditches (Baker et al. 2006). We therefore excluded Delmarva watersheds from chemical and temperature analyses. Upland watersheds in the Chester, Elk, Brandywine-Christina and Broadkill-Smyrna basins (see Eastern Shore division line in Fig. 22) were included in hydrologic analyses as agricultural drainage ditches in the northern and central Delmarva are relatively rare.

Methods

Hydrologic data

Data used to assess hydrologic regimes were derived from United States Geological Survey (USGS) stream gage records (USGS 2009a). Collected records of mean daily discharge were limited to the years 1996-2006, inclusive, to coincide with the year that our selected land use coverage represented (2001). If the available record for a given site-year was <90% complete, data from that year were excluded from calculations. Further, if the time increment between successive readings was adjusted within the retrieved record, data from the transitional year were omitted.

Six hydrologic metrics were calculated to quantify flow regime change with a primary focus on characterization of high (spate) or acute low flow event frequency, magnitude or duration; metrics have demonstrated previous success in detecting flow regime alteration in an urban setting (Poff et al. 2006, Konrad et al. 2005, Roy et al. 2005). All variables were averaged across complete years of record. Spate frequency was quantified by counting the occurrence of events where maximum mean daily discharge exceeded three times the monthly median daily discharge (Olden and Poff 2003). We initially considered the metric T_{Qmean} (Konrad et al. 2005), the fraction of time in which discharge exceeded the monthly mean, to assess spate duration. However, T_{Qmean} was highly correlated with surge frequency (Pearson correlation coefficient=0.84, $p<0.0001$). Thus the mean duration of surges (time elapsed while above 3× the monthly median) was used instead. An acute low flow event was defined as discharge falling below 25% of the annual median (Roy et al. 2005). Both the frequency of occurrence and annual maximum duration of acute low flow events

were calculated and used as metrics. The maximum and minimum observed daily discharges were divided by the watershed area (km^2) to provide normalized high- and low-flow magnitude metrics (Olden and Poff 2003, Poff et al. 2006).

Chemical data

Stream water chemistry data were obtained from three sources. Sampling protocols and assessed parameters varied among datasets so each was assessed separately to determine if results were consistent. The largest dataset was provided by rounds one (1995-1997) and two (2000-2004) of the Maryland Biological Stream Survey (MBSS; Klauda et al. 1998), a statewide stream monitoring program that includes assessment of water chemistry. Water quality sampling in the MBSS protocol includes one collection during spring (March 1-April 30) when flows are low enough to allow macroinvertebrate sampling (i.e., approximately baseflow). Although most MBSS reaches were sampled once, about 20% were sampled 2-10 times over the course of both rounds. The total maximum daily load program of the Maryland Department of the Environment (MDE) provided the second largest stream chemistry dataset (MDE 2009). In the MDE program, water samples were collected ≥10 times at each site throughout the year between 1997 and 2006 regardless of flow or weather conditions. The smallest dataset was provided by the Baltimore County Watershed Management and Monitoring program (Baltimore County Department of Environmental Protection and Resource Management 2008); the dataset included samples collected during baseflow conditions 6-10 times annually in the spring, summer, and fall of 2003-2006.

All samples from each program were subjected to laboratory chemical analysis; laboratory protocols followed those outlined by the United States Environmental Protection Agency (USEPA 2001). The variables analyzed included: conductivity, concentrations of sulfate (SO_4), dissolved organic carbon (DOC), total nitrogen (TN), and total phosphorous (TP) in the MBSS dataset; conductivity, total suspended solid (TSS), TN, DOC, and chlorophyll a concentrations in the MDE dataset; and hardness, total solid (TS), SO_4, TN, and TP concentrations in the Baltimore County dataset.

We assessed changes in chemical composition (the dependent variables) along impervious surface gradients (the independent variables) for variables expected to be affected by urbanization. If the Pearson correlation coefficient between two dependent variables within a dataset exceeded 0.75, only one variable was assessed to minimize redundant analyses. Dependent variable values were averaged across collections for sites that were sampled multiple times.

Temperature data

Water temperature data were derived from the MBSS round two dataset. Temperature loggers were deployed during the spring sampling period and programmed to read every twenty minutes starting on June 1. Terminal dates varied between August 25 at the earliest and September 18 at the latest. Records were visually assessed in a graphing program to determine if desiccation had likely occurred; data from loggers that appeared to temporarily go dry as well as those collected dry were excluded from analyses.

Four temperature variables were calculated: mean, maximum, the number of days in which a temperature surge (presumably associated with a spate) occurred and the

mean observed surge duration. A surge was defined as an increase of ≥1.3 ºC between readings and was assumed to persist until temperatures had reached ≤1.3 ºC of the pre-surge temperature (Nelson and Palmer 2007). The number of days where a surge was recorded was standardized to account for variable record lengths by multiplying the value by the total record length in days and dividing by 93 (i.e. the record length in days between June 1 and August 30).

Geographic data and procedures

Watersheds corresponding to each stream sampling location were delineated using GIS; watershed impervious cover was quantified for each gage location and sampling point. A sink-corrected 30 m resolution national digital elevation dataset (USGS 2009b) was used to determine watershed boundaries above each point coordinate. The impervious surface cover layer was provided by the National Land Cover Database (NLCD), a raster dataset representative of the year 2001 (USEPA 2008). Each 30×30 m pixel in the NLCD dataset includes an estimate of percent impervious cover between 0 and 100; these values were summarized to calculate total impervious cover at the scales described below. We also calculated percent agricultural cover (sum of pasture and row crop classes) from the land use layer of the NLCD dataset to exclude highly agricultural watersheds from certain temperature and chemistry analyses. Percent physiographic composition of each site was calculated from the Level III Ecoregion layer provided by United States Environmental Protection Agency (USEPA 2007).

The percent impervious surface cover at the watershed, network buffer, and local scales (Fig. 23) relative to the gage or sample point were calculated for use as

predictor variables. The watershed scale was defined as the percent impervious surface cover of the entire catchment. For the network buffer scale, we calculated the percent impervious cover in a buffer zone that was 200 m perpendicular to both sides of the entire stream channel network upstream of the sampling point. Impervious cover at the local scale represented land in the network buffer zone but within a 2 000 m radius upstream of the gage or sample point. Stream channels were derived from the flowline component of the National Hydrography Dataset Plus dataset (Horizon Systems Corporation 2009), which includes all perennial stream channels mapped at a 1:100 000 scale. Percent agricultural cover at the watershed and network buffer scales was also calculated for each site.

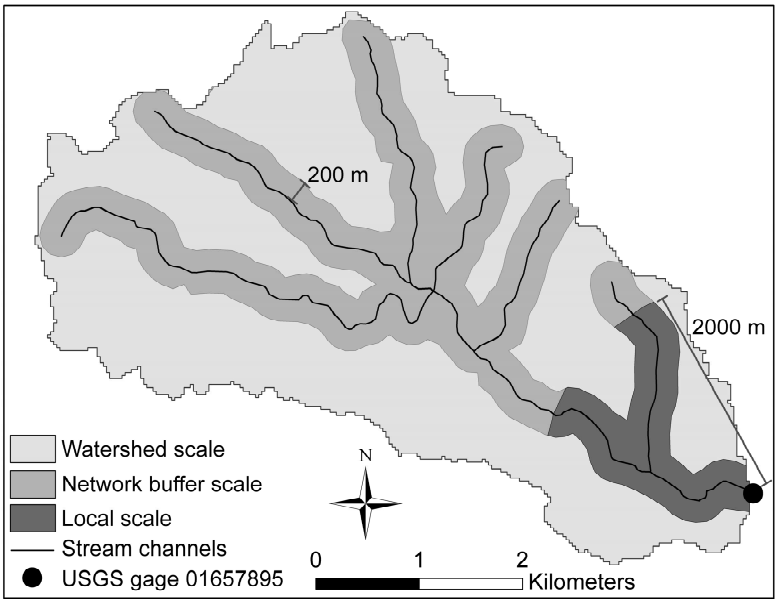

Figure 23. Map of the Powells Creek (Virginia) watershed illustrating the three spatial scales in which percent impervious surface cover estimates were calculated.

Statistical analyses

Sampling sites from each dataset met a number of criteria established *a priori* before being included in the statistical analyses. Only fifth-order ($\leq$282 km^2;

Knighton 1998) or smaller catchments were selected. Watersheds with a major impoundment on the main stem of the stream network were excluded. Further, each catchment was ≥95% within either the Coastal Plain or Piedmont (the majority were 100% within either province). Table 13 shows the final number of watersheds in each dataset delineated by physiographic province. Considerable disparities in watershed area existed among some of the datasets; Piedmont watersheds were somewhat larger than the Coastal Plain sites, although the differences were inconsistent among the datasets (Fig. 24).

Table 13. Sample size of each dataset. Values in parentheses indicate the number of samples remaining after highly agricultural sites (≥40% coverage at the watershed scale) were excluded for certain analyses.

Dataset	Sub-dataset	Coastal Plain	Piedmont
Hydrologic		63	107
Chemical			
	Maryland Biological Stream Survey	374 (320)	631 (138)
	Maryland Department of the Environment	44 (43)	149 (37)
	Baltimore County	15 (10)	91 (43)
Temperature		187	164

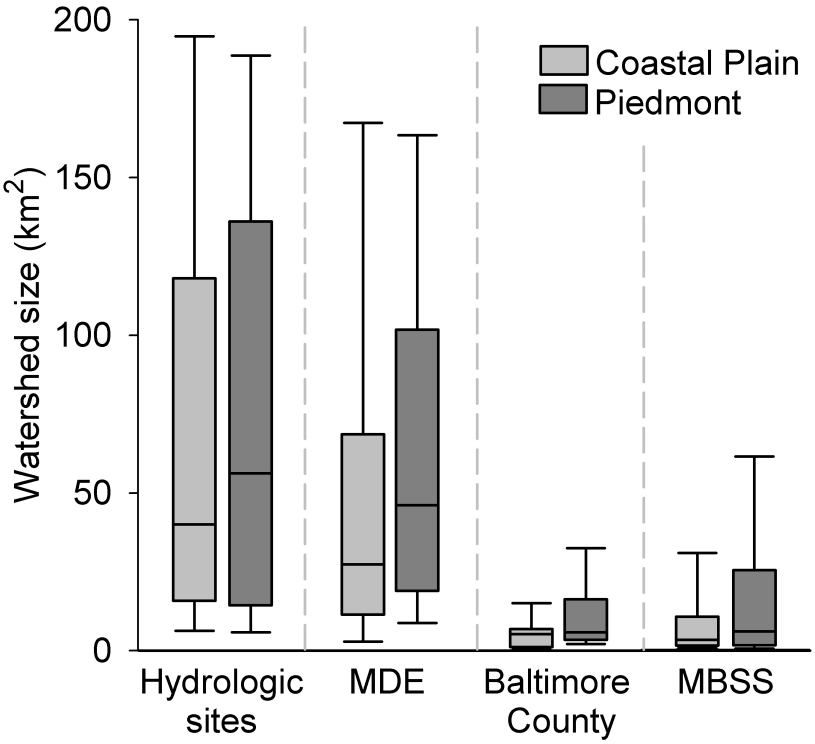

Figure 24. Distribution of watershed sizes among datasets.

The template statistical test for each quantified variable was an analysis of covariance (ANCOVA) model with province (Coastal Plain or Piedmont), impervious surface cover, and an interaction term as predictor variables. Prior to the ANCOVA, the most appropriate scale of impervious surface cover (watershed, buffer, or local) was chosen by running each model and selecting the one with the lowest Aikake's Information Criterion (AIC) score (Burnham and Anderson 2002). Normality of residuals was visually assessed with normal distribution probability plots; data were $\log_{10}$-transformed to approximate normality where necessary. Variance homogeneity with respect to the physiographic province term was tested using Levene's test (Levene 1960). If variances were highly ($p<0.01$) heterogeneous, an ANCOVA with variance heterogeneity incorporated into the model was run. The assumption of

variance homogeneity was also explored with respect to the continuous variable by plotting the residuals against the predicted value separately for each province and visually assessing if variances increased substantially along the gradient (Zar 1999).

Data were filtered, transformed and/or blocked where appropriate. Temperature data were derived from five years (2000-2004) and were assumed to be affected by inter-annual climatic variability. We therefore blocked all temperature analyses by year. Further, stream water temperature attributes vary by watershed size (Vannote and Sweeney 1980, Nelson and Palmer 2007), and streams in the MBSS dataset were right-skewed with respect to this variable (i.e. they are mostly small watersheds with a minority of larger sites). Thus for all temperature analyses $\log_{10}$-transformed watershed size (km^2) was included as a predictor variable. A number of chemical parameters (TN, TP, DOC, and chlorophyll a concentrations) are strongly influenced by agricultural land use but are also known to increase along a forested to urban land use gradient (King et al. 2005); sites with ≥40% agricultural cover at the watershed scale were therefore excluded for these analyses. Further, sites with ≥40% agricultural cover in the network buffer zone were excluded from all temperature analyses to remove potential confounding effects from a lack of shading in agricultural riparian zones. Therefore, the environmental attributes of test sites varied somewhat depending on the variable being tested. Though all consisted of small streams that were entirely within one of two provinces, highly agricultural watersheds were included for some tests but not others. Such variable criteria were necessary in order to isolate the effects of urbanization.

In each dataset, certain sites were located some distance upstream of others (hereafter referred to as nested) and we were concerned that such non-independence among sample units may have affected results. We explored this possibility by performing permutations of ANCOVA models on randomly selected non-nested subsets of data for each high flow event variable. The hydrologic dataset included 57 nested sites in 19 groups. Therefore datasets with 132 non-nested sites could be derived (113 sites were not nested). Two permutation procedures with 1 000 iterations each were run: one with data subsets consisting of one randomly selected site from each nested group along with the 113 original non-nested sites and the other with 132 randomly selected nested and non-nested sites (to see if any disparity in results could be attributed to a reduction in sample size). The percentage of p-values below α=0.05 and mean p-value for each term (province, impervious surface and interaction) from both permutation procedures were calculated to determine if nestedness and/or a reduction in sample size affected statistical outcome.

Results

Hydrologic change

Province-specific differences in hydrochemical responses along impervious surface gradients were observed for all variables that characterized high flow conditions. ANCOVA models for surge frequency (df=3, F=98.8, $p<0.0001$; $r^2=0.64$), $\log_{10}$-transformed duration (df=3, F=17.5, $p<0.0001$; $r^2=0.24$), and maximum daily flow (df=3, F=29.1, $p<0.0001$; $r^2=0.35$) were statistically significant and the continuous, province, and interaction terms were significant in each model (Table 14, Fig. 25). Impervious cover at the network buffer scale proved the best model for

surge frequency and duration, while the impervious cover at the watershed scale was selected for daily maximum flow. Spates in rural Piedmont streams were more frequent, of shorter duration and annual maximum flows were larger relative to those observed in rural Coastal Plain streams (Table 15). However, increasing the impervious surface cover affected Coastal Plain streams to a greater degree such that regression models converged at high levels of impervious cover (Fig. 25).

Table 14. Hydrologic variable ANCOVA model details. Only models that were found to be statistically significant are shown.

	% Impervious surface		Province		Interaction	
Variable	F	p-value	F	p-value	F	p-value
Number of surges	257.1	<0.0001	38.5	<0.0001	9.8	0.0021
(log_{10}) Surge duration (min)	23.0	<0.0001	29.1	<0.0001	4.1	0.0452
Max. daily flow ($m^3 s^{-1}$) / watershed size (km^2)	73.9	<0.0001	16.8	<0.0001	5.0	0.0275
Max. duration of low flow events (min)	6.0	0.0582	3.2	0.0741	3.8	0.0533

Low flow event attributes did not appear to vary between provinces or change substantially along impervious surface gradients. The log_{10}-transformed frequency (df=3, F=1.12, p=0.3422; network buffer scale) of low flow events and minimum annual daily flow (df=3, F=0.3, p=0.8184; watershed scale) ANCOVA models were not found to be statistically significant. Analysis of log_{10}-transformed low flow event duration did reveal significance in the full ANCOVA model (df=3, F=3.5, p=0.0176, r^2=0.06; network buffer scale), however, none of the individual terms were independently significant (Table 14).

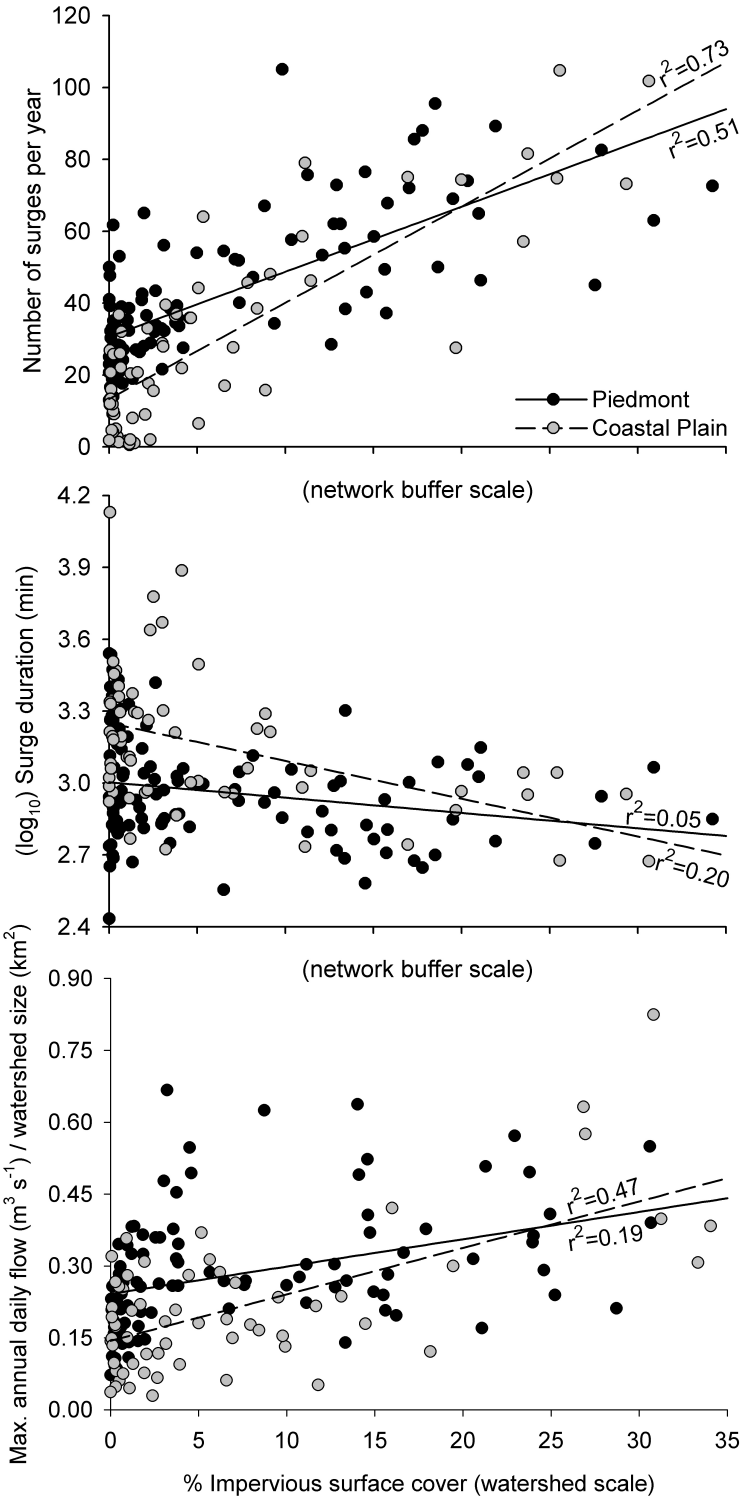

Figure 25. Relationships between high flow hydrologic metrics and impervious surface cover delineated by physiographic province.

Table 15. Comparisons of intercepts and slopes (±95% confidence intervals) for significantly different parameters. Values with a greater actual (for intercepts) or absolute (for slopes) magnitude are in bold; slopes not significantly different from zero are italicized.

		Intercept		Slope	
Dataset	Parameter	Coastal Plain	Piedmont	Coastal Plain	Piedmont
Hydrologic	Number of surges	13.3±4.3	**30.6±3.5**	**2.7±0.4**	1.8±0.3
	$\log_{10}$ Surge duration (min)	**3.3±0.1**	3.0±0.1	**-15.8±8.1 (×10^{-3})**	-6.4±5.3 (×10^{-3})
	Maximum daily flow (m^{3}s^{-1}/km^2)	1.4±0.4 (×10^{-1})	**2.4±0.3 (×10^{-1})**	**9.7±2.7 (×10^{-3})**	5.7±2.4 (×10^{-3})
Chemical (MBSS)	Conductivity (µS/cm)	100.5±16.5	**183.8±11.3**	-	-
	SO_4 (mg/L)	**14.3±1.1**	9.6±0.6	-	-
	$\log_{10}$ DOC (mg/L)	**5.1±0.3 (×10^{-1})**	2.8±0.5 (×10^{-1})	-	-
	TN (mg/L)	6.5±0.9 (×10^{-1})	**17.5±2.0 (×10^{-1})**	-	-
	$\log_{10}$ TP (mg/L)	**-1.6±0.1**	-1.8±0.1	*-1.3±3.9 (×10^{-3})*	**7.9±5.3 (×10^{-3})**
Chemical (Baltimore County)	Hardness (mg/L)	-	-	4.0±2.1	**8.2±1.3**
	TS (mg/L)	-	-	7.5±4.8	**13.0±1.6**
	$\log_{10}$ TP (mg/L)	**3.5±0.5 (×10^{-2})**	1.6±0.4 (×10^{-2})	*-1.4±3.4 (×10^{-4})*	**3.2±2.9 (×10^{-4})**
Chemical (MDE)	Conductivity (µS/cm)	119.0±41.9	**202.7±22.3**	-	-
	TN (mg/L)	8.4±1.5 (×10^{-1})	**17.3±2.5 (×10^{-1})**	-	-
	$\log_{10}$ DOC (mg/L)	**7.7±0.4 (×10^{-1})**	3.4±0.7 (×10^{-1})	*-2.6±3.8 (×10^{-3})*	**8.3±5.6 (×10^{-3})**
	$\log_{10}$ Chlorophyll a (µg/L)	**6.4±1.5 (×10^{-1})**	3.6±1.3 (×10^{-1})	-1.6±1.5 (×10^{-2})	**1.2±0.9 (×10^{-2})**
Temperature	Mean (ºC)	**20.2±0.8**	17.8±0.7	3.2±2.3 (×10^{-2})	**7.6±2.7 (×10^{-2})**
	Maximum (ºC)	**26.3±3.3**	22.9±1.5	1.1±0.5 (×10^{-1})	**1.7±0.5 (×10^{-1})**
	$\log_{10}$ Surge duration (hr)	**2.3±0.2**	2.1±0.2	2.2±0.8 (×10^{-2})	**3.3±0.9 (×10^{-2})**

Chemical change

Chemical composition varied between physiographic provinces and multiple variables were correlated with surface imperviousness. However, the degree of change along impervious surface gradients varied between provinces in only a minority of parameters. In the MBSS dataset, overall ANCOVA models were significant for conductivity (df=3, F=255.6, $p<0.0001$, $r^2=0.44$; network buffer scale), SO_4 (df=3, F=121.2, $p<0.0001$, $r^2=0.27$; watershed scale), log_{10}-transformed DOC (df=3, F=44.1, $p<0.0001$, $r^2=0.23$; watershed scale), and log_{10}-transformed TP (df=3, F=11.0, $p<0.0001$, $r^2=0.10$; watershed scale). The province and impervious surface cover (watershed scale) terms were also significant in a mixed model for TN (Table 16). While the impervious surface and province terms were significant for most parameters, only the log_{10}-transformed TP model included a significant interaction term. Rural Piedmont streams were more conductive and had higher concentrations of TN, while rural Coastal Plain streams exhibited higher concentrations of SO_4, DOC, and TP (Table 15). Impervious surfaces appeared to cause TP to increase in the Piedmont, but not in the Coastal Plain (the slope in the Coastal Plain was not significantly different from zero).

Results from the Baltimore County dataset included some interactive effects between province and impervious surface gradients (Tables 15 and 16). ANCOVA models for hardness (df=3, F=59.4, $p<0.0001$, $r^2=0.67$; network buffer scale), TS (df=3, F=94.4, $p<0.0001$, $r^2=0.76$; network buffer scale), SO_4(df=3, F=22.0, $p<0.0001$, $r^2=0.55$; watershed scale), and log_{10}-transformed TP (df=3, F=5.1,

Table 16. Chemical ANCOVA model details. Only models found to be statistically significant are shown.

		% Impervious surface		Province		Interaction	
Dataset	Variable	F	p-value	F	p-value	F	p-value
MBSS							
	Conductivity (µS/cm)	705.1	<0.0001	68.5	<0.0001	0.4	0.5052
	SO_4 (mg/L)	200.7	<0.0001	61.9	<0.0001	0.5	0.4622
	$\log_{10}$ DOC (mg/L)	6.1	0.0136	45.2	<0.0001	0.8	0.3798
	TN (mg/L)	15.3	0.0001	93.8	<0.0001	0.0	0.9406
	$\log_{10}$ TP (mg/L)	3	0.0868	27.6	<0.0001	5.7	0.0180
Baltimore County							
	Hardness (mg/L)	51.6	<0.0001	0.1	0.8643	6.2	0.0146
	TS (mg/L)	83.8	<0.0001	0.1	0.7431	6.1	0.0154
	$\log_{10}$ TP (mg/L)	6.6	0.0136	14.9	0.0004	13.6	0.0006
MDE							
	Conductivity (µS/cm)	149.0	<0.0001	12.1	0.0006	0.3	0.6181
	TSS (mg/L)	5.0	0.0283	2.2	0.1442	0.1	0.7686
	TN (mg/L)	14.9	0.0003	42.4	<0.0001	2.2	0.1466
	$\log_{10}$ DOC (mg/L)	2.8	0.0968	110.7	<0.0001	10.5	0.0018
	$\log_{10}$ chlorophyll a (µg/L)	0.2	0.6993	8.7	0.0043	9.3	0.0032

p=0.0041, r^2=0.25; watershed scale) were statistically significant, while the model for TN was not (df=3, F=0.9, p=0.4350; watershed scale). Hardness and TS concentrations were not significantly different between provinces in rural streams yet both increased more along impervious surface gradients in the Piedmont. The TP

model concurred with findings from MBSS streams; TP increased along an impervious surface gradient in the Piedmont, but not in the Coastal Plain.

Trends observed in MDE models largely reflected those of the MBSS dataset (Tables 15 and 16). Conductivity (df=3, F=50.5, $p<0.0001$, $r^2=0.48$; watershed scale), TSS (df=3, F=3.3, p=0.0248, $r^2=0.13$; network buffer scale), and TN (df=3, F=35.7, $p<0.0001$, $r^2=0.62$; network buffer scale) were statistically significant as well as some terms in the log_{10}-transformed DOC (network buffer scale) and log_{10}-transformed chlorophyll-a (network buffer scale) mixed models. TN concentrations and conductivity differed between provinces in rural streams, and both increased along impervious surface gradients but neither model included a significant interaction term. In contrast, log_{10}-tranformed DOC and log_{10}-transformed chlorophyll-a concentrations were significantly higher in Coastal Plain rural streams and only increased along an impervious surface gradient in the Piedmont.

Temperature change

Most temperature attributes were affected by impervious surfaces to a greater degree in Piedmont streams. For each tested temperature the network buffer was the selected scale of impervious surface cover and at least one mixed model term was found to be significant (Table 17). Mean and maximum temperatures were higher in rural Coastal Plain streams yet each increased to a greater degree along the impervious surface gradient in Piedmont streams (Fig. 26, Table 15). Similarly, the mean duration of temperature surges increased along an impervious surface gradient but significantly more so in Piedmont streams. The only parameter that did not differ

between provinces or exhibit variable relationships with impervious surfaces between provinces was the number of days in which a surge occurred.

Table 17. Details of temperature variable ANCOVA models.

	% Impervious surface		Province		Interaction	
Variable	F	p-value	F	p-value	F	p-value
Mean (ºC)	35.2	<0.0001	134.7	<0.0001	7.2	0.0079
Maximum (ºC)	51.0	<0.0001	60.8	<0.0001	6.5	0.0113
$\log_{10}$ Surge duration (hr)	70.2	<0.0001	5.2	0.0237	5.5	0.0196
Number of days with a surge	84.8	<0.0001	1.0	0.3199	3.8	0.0529

Effect of nested watersheds

Permutation of ANCOVA models for high flow event variables suggested that the presence of nested watersheds did not substantially affect statistical outcomes (Table 18). For surge frequency, the p-value for each model term was below 0.05 in the nested removal permutation procedure for 100% of the iterations, which matched conclusions using the full dataset. Though the impervious surface and province terms were statistically significant in 100% of the iterations for surge duration and maximum daily flow, the interaction term was not found to be statistically significant for the majority of iterations. However, randomly reducing the sample size produced a similar effect.

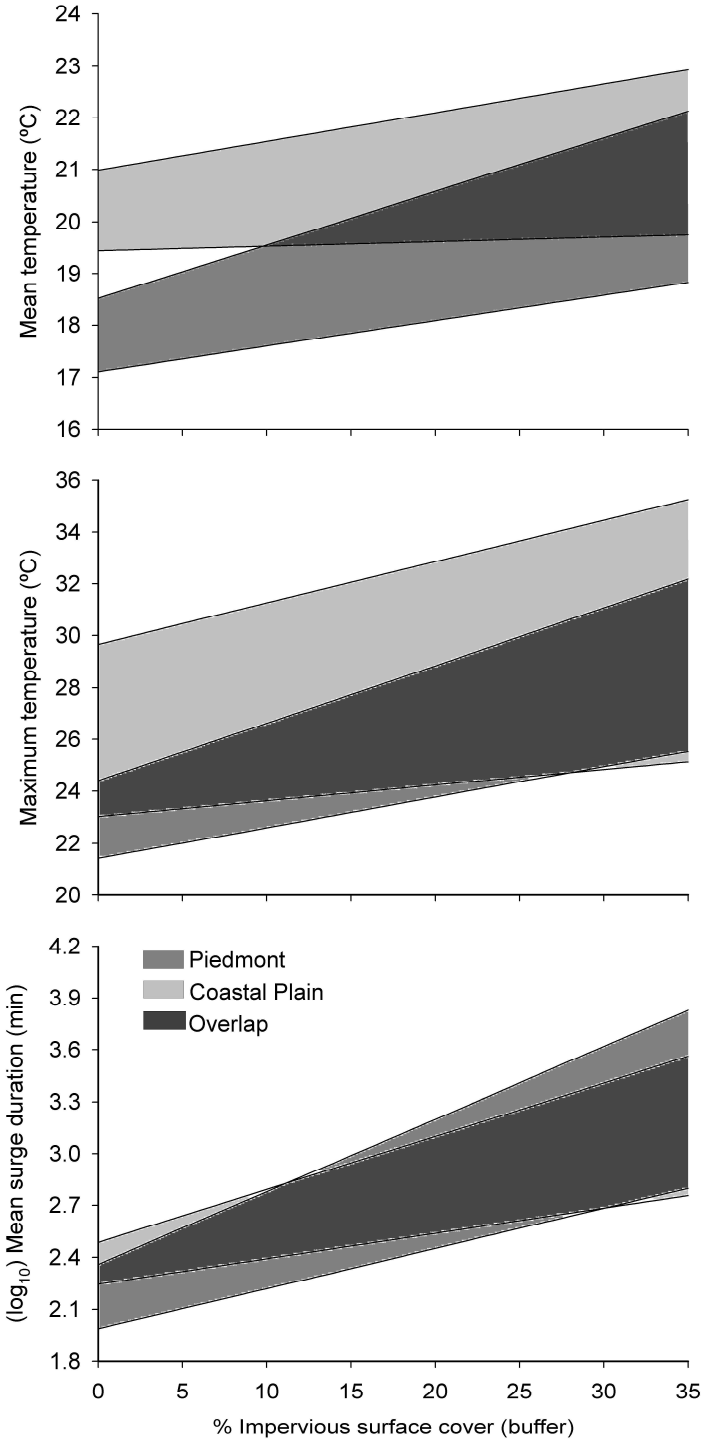

Figure 26. Relationships between temperature variables and impervious surface cover delineated by physiographic province. Shaded areas represent 95% confidence intervals of regression parameters.

Table 18. Permutation procedure details for high flow event ANCOVA models. 'Nested removal' refers to the iterative process where only nested watersheds were targeted for removal; the final random subset represented only independent sites (132 out of 170). 'Random removal' represents iterations of the models where 132 sites were randomly chosen. Both processes represent 1000 iterations.

		Nested removal		Random removal	
Variable	Parameter	Mean p-value	% <0.05	Mean p-value	% <0.05
Number of surges	ISC (buffer)	<0.0001	100	<0.0001	100
	Province	<0.0001	100	<0.0001	100
	Interaction	0.0018	100	0.0109	95.1
(log) Mean duration of surges	ISC (buffer)	<0.0001	100	0.0001	100
	Province	<0.0001	100	<0.0001	100
	Interaction	0.1081	2.8	0.1037	31.5
Maximum daily flow/watershed size	ISC (buffer)	<0.0001	100	<0.0001	100
	Province	0.0005	100	0.0007	100
	Interaction	0.3415	0	0.0881	52.4

Discussion

Our results demonstrate that the magnitude of urbanization-induced physicochemical change in streams may be strongly influenced by physiography. As previous biological assessments (Morgan and Cushman 2005, Goetz and Fiske 2008, Utz et al. 2009) have suggested, thermal properties of streams were more affected by impervious surfaces in the Piedmont than in the Coastal Plain. However, contrary to what was expected, hydrologic attributes associated with high flow events are apparently affected by impervious surface cover to a greater degree in Coastal Plain systems. In further contrast, few chemical parameters showed province-specific degrees of change along gradients of impervious surface cover. Therefore physicochemical degradation caused by urbanization may vary among geoclimatic

settings, but not necessarily in a uniform predictable manner among environmental attributes.

The disparate patterns of change along impervious surface gradients caused interregional homogenization of many physicochemical properties. For example, temperatures in naturally cooler Piedmont streams were more strongly elevated by impervious surfaces relative to those in the Coastal Plain. As a result, temperature regimes became increasingly similar between regions as urbanization increased. Comparable patterns of interregional congruence with increasing impervious cover were also observed for hydrologic attributes associated with spates. Therefore urban development appears to cause a loss of physicochemical diversity at the interregional spatial scale. Such trends make intuitive sense: as urbanization grows, impervious surfaces prevent water from interacting with the surficial and shallow geologic attributes that render physiographic regions distinct. The loss of physicochemical diversity parallels, and could potentially contribute to, the homogenization of biotic assemblages at the landscape scale also observed in urban streams (Roy et al. 2005, Scott 2006).

The dissimilar hydrogeologic properties of the two provinces suggest a possible mechanistic explanation of the observed differences in hydrologic response to impervious surface cover. A comparison of published results from long-term intensive watershed studies conducted in the Piedmont (Dougherty et al. 2007) and Coastal Plain (Correll et al. 1999) provinces suggest that the observed differences in hydrologic responsiveness at zero imperviousness (Fig. 25) should not be attributed to differences in hydroclimatology. Dougherty et al. (2007) reported long-term (1979-

2002) annual precipitation and runoff for four gaged headwater basins in the Occoquan River watershed were 983 mm and 353 mm, respectively, while Correll et al. (1999) reported very similar values (1080 mm and 332 mm, respectively) for six subwatersheds in the Rhode River watershed for the 25-year period from 1972-1996. The modest differences (< 10%) in hydroclimatological conditions between these systems appear inconsistent with the magnitude of the hydrologic differences shown in Table 15.

Our results showing that the number of surges and the maximum daily flows are significantly higher in Piedmont than in Coastal Plain streams with zero imperviousness is in general agreement with regional flood frequency equations developed for Maryland streams by Dillow (1996) that predict higher flood magnitudes for Piedmont streams than for their Coastal Plain counterparts, all else being equal; for comparable 10 mi^2 watersheds with 100% forest cover, the peak discharge with a 2-year return period for a Piedmont stream is 557 cfs, compared to 206 cfs for a stream in the Western Coastal Plain.

Shallow basement rocks, relatively steep gradients, and soils with low infiltration capacity in the Piedmont (Swain et al. 2004) likely facilitate frequent, high magnitude, short duration floods associated with moderate precipitation events as is evident in our results. In contrast, the extensive depth of unconsolidated sediments, relatively low topographic relief, and pervious soils of the Coastal Plain (Ator et al. 2005) may attenuate to some degree the small, recurrent floods that characterize the average response of Piedmont streams. Therefore, replacing natural or agricultural land with impervious surfaces in the Coastal Plain induces greater hydrologic impact

relative to the Piedmont, all else being equal. Our results thus confirm the importance of considering the regional hydrogeologic context when assessing hydrologic shifts resulting from land use change (Poff et al. 2006a, b, Chang 2007). The same conclusion was reached for these same two physiographic provinces in interpreting water quality responses to agricultural cropping (Jordan et al. 1997b, Liu et al. 2000).

Differences in temperature regime response to impervious surface gradients between provinces may be explained by the hydrogeologic, geomorphic and climatic attributes that characterize each region. One means in which temperatures are elevated in urban streams is the delivery of spate runoff that has moved over impervious surfaces warmed by solar radiation (Herbs et al. 2008). Piedmont streams are naturally cooler, possibly due to spring seepage from basement rocks that exist only in the Piedmont and/or by the slightly lower air temperatures (0.5-1.0ºC difference by monthly average; Maryland State Climatologist 2009) relative to the Coastal Plain. Therefore, spate runoff must reach a higher temperature to produce a detectable thermal impact in Coastal Plain streams. A second means of temperature elevation in urban streams is the removal of canopy cover that induces solar conduction of sediments in the wetted channel (LeBlanc et al. 1997, Krause et al. 2004). Coastal Plain streams tend to be deeper and water is often colored by dissolved organic material (blackwater streams; Mallin et al. 2004), both properties that may buffer solar radiation-driven sediment conduction. The above mechanistic explanations of ecoregion-specific thermal responses to urbanization are speculative and require further research. Regardless, our findings pertaining to thermal properties

further highlight the need to consider regional context when assessing impact in urban streams.

Contrary to hydrologic and thermal regimes, most chemical properties changed to a similar degree along impervious surface gradients between regions. The majority of chemical concentrations in rural streams differed significantly between the two provinces as previously observed (Kaufmann et al. 1991, Zipper et al. 2002, Stoddard et al. 2006). However, only total phosphorus was found to be consistently divergent in response to impervious surface gradients (with concentrations affected only in Piedmont streams) among datasets. A similar lack of interactive effect was observed in earlier work (Liu et al. 2000) between the same two regions, including some chemical species not tested in the current study though with a limited number of urbanized streams. Such an absence of significant differences between slopes is surprising, as interactive effects have been noted with other land use gradients. For instance, baseflow nitrate concentrations increase more per areal unit of agriculture in Piedmont streams relative to those of the Coastal Plain (Jordan et al. 1997a, b). The lack of province-urban gradient interaction could be attributable to the nature of the chemical data, as the majority of samples were collected during baseflow whereas most province-specific responses to urbanization appear to be (directly or indirectly) related to spate flows. Further research will be necessary to determine if pollutant concentrations vary between provinces during high flows.

Although our findings do not identify a single mechanism behind the disparate biotic responses to urbanization, they do confirm the use of biotic indicators to predict spatial variation in physicochemical degradation and may be used to generate specific

hypotheses. Ecologists have long recognized the importance of physiography in delineating community composition at the landscape scale (Tate and Heiny 1995, Johnson 2000, Duggan et al. 2002) and have consequently considered ecoregions when constructing indices of biotic integrity (IBI's; Stribling et al. 1998). However, our results suggest that if indicators respond differently to a landscape stressor among regions, potential physicochemical mechanisms should be explored before adjusting metrics in attempt to achieve interregional IBI homogeneity (i.e. Astin 2007, Southerland et al. 2007). Unfortunately, the diverse nature of biotic assemblages and physicochemical responses to urbanization in streams precludes identifying why Piedmont streams lose greater biodiversity along an urban gradient using our results alone. For instance, the higher relative increase in temperatures in Piedmont streams may be a potential driver (Sponseller et al. 2001, Wang and Kanehl 2003). Alternatively, the naturally low spate frequency and magnitude in rural to moderately urbanized Coastal Plain streams may buffer organisms from physical disturbances (Bond and Downes 2000, Roy et al. 2005, Gibbins et al. 2007a, b). The specific mechanism behind the observed biotic resiliency in the Coastal Plain may vary by assemblage or species and could involve multiple, interacting physicochemical responses.

Despite such unanswered questions, the diversity in physicochemical response to urbanization suggests that conservation and restoration efforts may be improved by taking physiographic context into consideration. Watershed management within a physiographic province could target those physicochemical attributes that are acutely vulnerable to change in order to increase the likelihood of maintaining a natural

environment in an urban setting. Our results suggest that conserving or restoring riparian vegetation for the purposes of shading to keep water temperatures cooler (DeWalle 2008) may be more pertinent in the Piedmont, while minimizing short duration flow events through mitigative structures (Dietz et al. 2007, Li et al. 2009) could serve to greater effect in moderately urbanized streams of the Coastal Plain. Further management insight could be gained by exploring the province-specific geomorphic responses to urbanization, as many restoration efforts target habitat improvement or bank stability (Bernhardt et al. 2005) and the geomorphic differences between the two provinces are substantial.

Our analyses did not consider, or treated coarsely, certain factors that complicate the effects of urbanization on streams. Agricultural development may impact multiple abiotic properties in streams, especially thermal and certain chemical properties such as nutrients (McTammany et al. 2007), though other effects (i.e. hydrologic) are subtle in comparison to urbanization (Poff et al. 2006a). While excluding watersheds with ≥40% agriculture (at the network buffer scale for temperature analyses) where appropriate reduced the likelihood that agriculture affected our results, sites with <40% could have been affected by agriculture to some degree. The disparity in watershed size distributions among datasets precludes some conclusions. For instance, it is unclear if the patterns in hydrologic responses to urbanization would be consistently observed in small (<10 km^2) streams. Recent efforts have highlighted that impervious surfaces directly connected to stream channels, or effective impervious (EI) cover, may serve as a better predictor of degradation than total impervious cover (Walsh et al. 2005, Wenger et al. 2008, Walsh et al. 2009). The

large spatial extent of our sites and lack of EI models for the entire region disallowed consideration of EI as a predictor. However, our findings are meant to represent a coarse survey of comparative physicochemical responses to urbanization between regions. The consistent trends observed despite the nature of the data suggest that further investigation would confirm our findings and identify additional province-specific patterns.

In summary, our results highlight the need for further interregional examinations of land use-stream ecosystem relationships. Though case study and local-scale efforts contribute substantially to our understanding of stream ecosystems in the urban environment, comparative regional approaches consistently (Potopava et al. 2005, Poff et al. 2006a, Sprague and Nowell 2008, this study) highlight interregional variability in patterns of physicochemical response to urbanization. Similar trends are observed when other classes of land use such as row crop agriculture are examined (Jordan et al. 1997a and b, Liu et al. 2000). Considering the diversity of geoclimatic settings at continental spatial scales (for instance, the 84 delineated ecoregions within the continental United States, USEPA 2007), the potential implications for watershed conservation and management are profound.

CHAPTER VI

INTERREGIONAL DIFFERENCES IN URBANIZATION-INDUCED GEOMORPHIC IMPACT IN STREAMS AND MACROINVERTEBRATE DISPERSAL DYNAMICS

Urbanization induces substantial geomorphic adjustment and, consequentially, benthic habitat alteration in streams. Decades of empirical studies have led to the creation of a predictive temporal framework of sediment deposition and channel morphometry dynamics following watershed urbanization (Paul and Meyer 2001, Walsh et al. 2005). Construction activity initially causes a pulse of hillslope sediment delivery and consequential aggradation which is followed by an indefinite period of reduced deposition and loss of fine sediment once urban expansion ceases (Wolman 1967, Allmendinger et al. 2007, Colosimo and Wilcock 2007). The ultimate reduction in fine sediments occurs because an increase in moderate magnitude flood events causes the effective downstream transport of movable particles (Pizzuto et al. 2000). Due to the eventual relative paucity of fine sediments and simultaneous increase in scouring flow events, active channels in urban streams typically increase in bankfull width and/or become incised (Gregory et al. 1992, Van Duin and Garcia 2006, Hardison et al. 2009).

Yet characteristic stream form and function varies substantially among landscapes, thus the severity of geomorphic adjustment following urbanization may be context-specific. Stream hydrology, morphometry, and benthic sediment composition is naturally structured by local geoclimatic attributes such as topographic relief, geologic setting, and climate (Rosgen 1996, Faustini et al. 2009). Interregional

comparisons demonstrate that such diversity in stream form likely alludes to differences in the degree of geomorphic degradation in urbanized streams. For instance, streams in the Central Great Plains and Central Basin and Range North American ecoregions may show no signs of channel enlargement following watershed urbanization (Short et al. 2005, Kang and Marston 2006). Furthermore, the proportion of benthic sediments composed of fine particles may increase over time in certain urban streams due to prolonged bank erosion (Short et al. 2005, Allmendinger et al. 2007), while in others sediment composition may remain relatively unchanged (Kang and Marston 2006). Therefore both the magnitude and nature geomorphic responses to urbanization exhibit heterogeneity among stream forms.

Consequently, aquatic biota may exhibit variable sensitivity to urbanization across stream forms due to differences in geomorphology. Physical disturbance induced by hydrologic adjustment is often determined to be the mechanistic driver of biotic integrity decline in urban streams (Roy et al. 2005, Knight et al. 2008). Yet lotic organisms possess behavioral adaptations to cope with natural flood events (Bunn and Arthington 2002) and the success of such strategies in urban-impacted streams may be related to the extent of habitat degradation. For example, aquatic invertebrates take refuge in patches of woody debris snags during elevated flows (Palmer et al. 1996, Angradi 1997, Hax and Golladay 1998), and wood abundance may decrease (Larson et al. 2001), remain unchanged, or increase (Short et al. 2005) once streams are urbanized. Additionally, benthos inhabiting streambeds of large, stable particles tend to recover from floods more rapidly than organisms in reaches composed of small, transportable material (Cobb et al. 1992, Imbert et al. 2005). Despite such

observations, efforts to deduce if certain geomorphic settings confer biotic tolerance to urbanization are absent .

The Coastal Plain and adjacent Piedmont ecoregions of eastern North America represent an example of interregional variation in stream ecosystem-scale sensitivity to urbanization. Recent bioassessments at the community (Morgan and Cushman 2005, Goetz and Fiske 2008) and taxon-specific (Utz et al. 2009, Utz et al. *In review*) scales demonstrate heightened biological intolerance to urbanization in Piedmont streams relative to those of the Coastal Plain. Subsequent assessments of hydrologic and thermal impact along gradients of impervious surface cover (ISC, a surrogate for urban land use that includes surfaces such as pavement and rooftops) exhibit ecoregion-specific abiotic degradation as well: temperatures increase relatively more along ISC gradients in Piedmont streams yet flood regime hydrology is altered to a greater degree in the Coastal Plain. Characteristic stream geomorphology also varies substantially between provinces (Table 19), thus geomorphic responses to urbanization may be region-specific as well. Though morphometric and sediment regime alteration in urban streams has been explored separately in both provinces (i.e. Leopold 1973, Allmendinger al. 2007, Hardison et al. 2009), studies that explicitly compare the degree of impact between ecoregions have not been conducted.

In order to determine if geomorphic adjustment caused by urbanization varies between the Coastal Plain and Piedmont, I quantified morphology and sediment transport dynamics within rural and urban streams of both provinces. Features presumed to be temporally static following the initial geomorphic adjustment phases in urban streams such as bankfull width, depth, and sediment structure were

considered in addition to temporally dynamic attributes such as sediment stability and deposition. Furthermore, the rates of macroinvertebrate recolonization in physically disturbed habitat patches were monitored to detect interregional differences in the ability of benthic communities to cope with disturbance. Due to previously observed disparate patterns in biological and

Table 19. Characteristic geomorphic attributes of watersheds and streams in the North American eastern Piedmont and Coastal Plain physiographic provinces*.

Variable	Coastal Plain	Piedmont
Watershed attributes		
Range of elevation above sea level (m)	60 to >500	0 to ~100
Landscape topography	Incised near stream channels to uniformly flat	Undulating ridges and valleys
Depth of bedrock	10-1000m below soil and unconsolidated sediment	1-2m below layer of soil
Stream attributes		
Gradient	Low	Moderate to low
Acidity	Poorly buffered and/or naturally acidic	Well buffered
Dominant channel sediments	Cobble, gravel, silt, sand and clay	Bedrock, boulder, cobble, and gravel

*-references: Thornbury (1965), Swain et al. (2004), Ator et al. (2005), and Colosimo and Wilcock (2007).

physicochemical responses to urbanization between provinces, I hypothesized that geomorphic degradation would be more pronounced in urban streams of the Piedmont relative to those in the Coastal Plain. Furthermore, I predicted that macroinvertebrate recolonization of disturbed habitat would be greater in Coastal Plain streams.

Methods

Site selection

A database of watershed-scale information on each 75m reach of stream (~8,900 locations) within the state of Maryland was referenced to randomly select rural and urban study sites in each province. Land cover (percent ISC and Anderson-1 level land use classes such as agriculture) at the watershed- and 200m riparian buffer-scale was quantified at each site; these data represented conditions during 2001 and were provided by the National Land Cover Database (USEPA 2008). Only 1.0-3.5 km^2 sized catchments that were entirely within the Piedmont or western shore of the Coastal Plain were included as candidates. Among these, sites with <0.5% ISC at the watershed- and buffer-scale were considered for rural sites, while the potential urban site pool included all catchments with 10-15% ISC at both spatial scales. From these two groups, five sites in each physiographic provinces were randomly selected (n=20 sites total) for possible inclusion in the study. Each selected site was visually assessed via satellite imagery taken during 2007 and construction permits for 2008 (Maryland Department of Planning 2008) to ensure that urban development had not ensued since 2001 or was planned for the near future. Finally, sites with substantially high agricultural cover (>75% at either spatial scale) and Coastal Plain sites where benthic sediment consisted entirely of sand and silt were excluded. Those selected for the study are shown in Fig. 27 and site watershed attributes among urban/rural and physiographic classes are provided in Table 20.

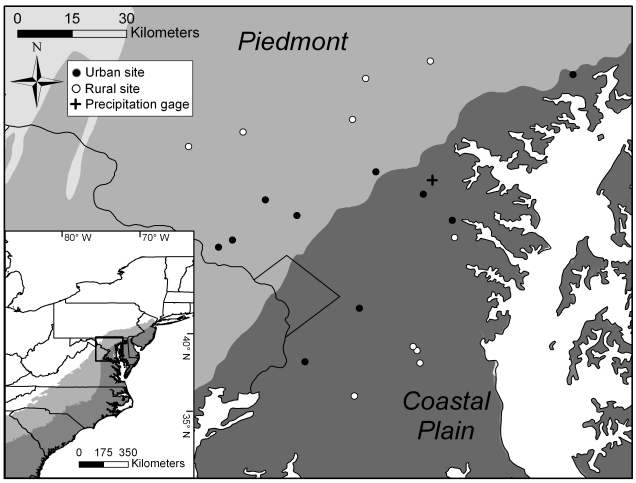

Figure 27. Map depicting the location of study sites and the Coastal Plain and Piedmont physiographic provinces of the eastern United States.

Table 20. Study site attribute information. Land cover values represent percentages at the watershed scale unless otherwise noted. Values shown are means ±1 standard error.

	Rural sites		Urban sites	
Variable	Piedmont	Coastal Plain	Piedmont	Coastal Plain
Watershed size (km^2)	2.5±0.7	2.4±0.7	3.0±0.2	2.9±0.7
Slope (%)	1.3±0.3	0.6±0.1	0.8±0.2	1.0±0.2
ISC	0.3±0.1	0.3±0.1	13.8±0.8	14.9±1.3
ISC (200m riparian buffer scale)	0.0±0.0	0.1±0.0	12.3±0.9	12.4±0.8
Agriculture	34.2±10.1	35.2±8.8	21.1±4.29	11.1±3.8
Forest	53.8±6.6	59.9±7.5	27.7±3.1	36.8±8.3
Wetlands	0.7±0.3	2.4±1.9	0.3±0.2	1.5±1.0

Morphometric and sediment surveys

Channel morphometry was quantified during the summer of 2008. At each site, ten cross sections were profiled at intervals spaced approximately ten times the channel width apart using a surveyor's level and stadia rod (Harrelson et al. 1994). Mean bankfull width and height were derived from profiles by plotting cross sections

in HEC-RAS 4.0 (USACE 2008) and estimating the extent of the active channel for each cross section; channel slopes were also quantified from these measurements. Active channel cross-section area was calculated by multiplying width by height. Site-specific averages of all aforementioned variables were averaged across cross sections. Counts of large woody debris delineated into size classes based on diameter and length were conducted within the entire extent of cross sections (i.e. a distance approximately 100× the channel width); these were summarized and scored as proposed by Stevenson and Bain (1999).

Wolman pebble counts (Potyondy and Hardy 1994) were also conducted to quantify benthic sediment structure. The intermediate axes of 200 randomly selected riffle sediment particles were recorded at each site. Cumulative frequency distributions derived from these data were used to determine site-specific median, 75^{th} and 90^{th} percentile particle sizes (hereafter the D_{50}, D_{75} and D_{90}, respectively).

Sediment movement and deposition

Sediment stability, deposition, and suspended/dissolved transport during flood events were measured over four months during the fall and winter of 2008-2009 (Fig. 28). Five site visits spaced roughly three weeks apart (anticipated precipitation occasionally delayed collection events) were made during baseflow conditions to collect data for each of the three procedures described below.

Bed stability was quantified using tracer sediment movements following the partial methodology of Townsend et al. (1997). At each site, painted particles corresponding to the local D_{75} and D_{90} (10 per size class) were deployed in a line perpendicular to flow within a riffle reach that was at least 10m long. The starting

point was marked with surveying flags secured above the bank. During each subsequent visit, the distance of each transported particle was recorded and those displaced or lost were replaced at the starting point. A scoring system was derived to quantify bed stability: unmoved particles received a score of 0, those that moved <1m scored a 1, movement distances between 1 and 10m scored a 2, and particles that were not recovered received a score of 3. The total score per size class per visit per site was summed as a measure of bed stability. Movement scores were averaged between D_{75} and D_{90} groups per visit per site as preliminary analyses demonstrated that differences in scores between size classes were negligible.

Sediment deposition was estimated by deploying passive *in situ* traps described by Hedrick et al. (2005). The trap design consisted of a 5cm long piece of 10.16cm diameter schedule 40 PVC pipe that was capped on one end, placed in a housing apparatus and filled with 12-25mm painted marble (anchor rocks). Apparatuses were buried so that traps were level with wetted riffle hyporheic sediments. During each site visit, traps were lifted from the housing unit and the contents were collected. Samples were dried in an oven and the anchor rocks were removed and weighed. The remaining contents were sorted in 6 stacked sieves (8, 4, 2, 1, 0.5, and 0.25mm mesh) using a mechanical shaker and the mass of each size class was recorded. Total mass and median particle size (by mass) was quantified for each sample. Additionally, the proportional volume of available space filled by deposited sediments was determined using the equation:

$$(\text{Sample mass}/1.7\text{g}\cdot\text{cm}^{-3})/[405.2\text{cm}^3 - (\text{Anchor rock mass}/2.6\text{g}\cdot\text{cm}^{-3})]$$

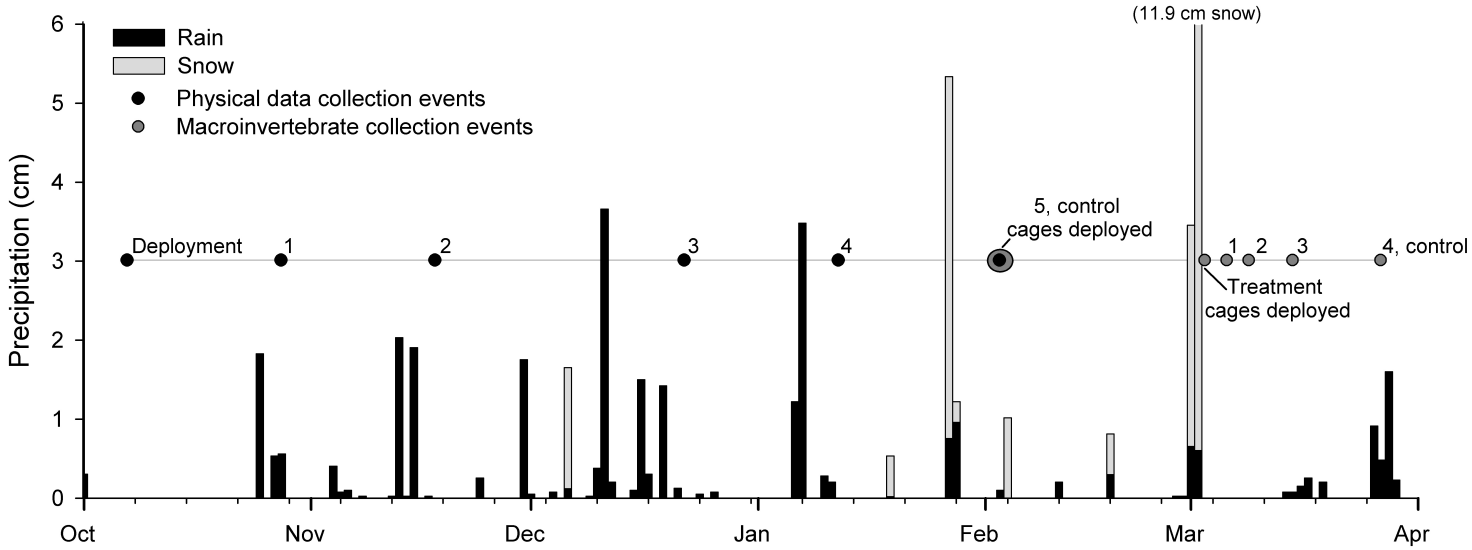

Figure 28. Study timeline and precipitation record. Numbers on the timeline adjacent to points denote collection events. Precipitation records were derived from gages at Baltimore/Washington International airport, the location of which is shown on Fig. 27.

where 1.7g·cm^{-3}= the density of dry sand and gravel of mixed rock composition, 405.2cm^{3}= the trap volume and 2.6g·cm^{-3}= the density of marble.

Floodwater suspended and dissolved solid concentrations were sampled via passive water collection during elevated flow events following the methodology of Schoonover et al. (2007). Collection apparatuses consisted of 500ml plastic bottles with a 3mm water intake hole near the top of the bottle and a 2mm hole on the lid. A piece of iron rebar was secured in the streambed and bottles were fastened to the rebar using hose clamps and cable ties. Intake holes at the time of deployment were 15cm above the baseflow water level. If a bottle was filled during the three week interim period, it was collected and replaced. Total suspended and dissolved solid (TSS and TDS, respectively) concentrations were measured in the laboratory. Conductivity and chloride concentrations were also measured to permit comparisons of floodwater chemistry with respect to these common urban water quality indicators.

Benthic macroinvertebrate colonization

Benthic macroinvertebrate recolonization dynamics within a patch of physically disturbed habitat were quantified at each site during the early spring of 2009 (see Fig. 28 for the study component timeline). Uniform patches of habitat were created by filling 25×25×5cm mesh (12mm grade) baskets with local sediments. One basket per site was filled with wetted channel sediment and placed within a riffle between February 2nd-3rd; these served as control patches at the terminus of the study. On March 3rd and 4th , four treatment baskets per site were filled with channel sediments, vigorously shaken while submersed in stream water and further disturbed by pouring

~30L of water on the apparatus from a vertical distance of 0.75m while placed on the bank. Each basket was then buried level with the wetted riffle hyporheic zone. One randomly selected treatment basket was removed from the channel and shaken in water within a D-net after being deployed for 3, 6, 12, and 24 days; contents of the control basket were also collected 24 days after the treatment baskets were set (i.e. 53 days since deployment). Samples were preserved in ethanol.

All macroorganisms other than Oligochaete worms were sorted from debris and each individual was identified to genus except for Chironomid flies, which were identified to subfamily. Two measures of treatment basket recolonization relative to site-specific control samples were quantified: the Bray-Curtis similarity based on presence/absence taxonomic data and the density of organisms per basket.

Statistical analyses

Significant differences among treatment groups were detected using two-factor analysis of variance (ANOVA) models. The three model components included a physiographic province term, a rural/urban dichotomous class term, and a province×rural/urban interaction term. Variables assumed to be related to watershed size (i.e. bankfull width, height and cross-section area) were standardized by dividing the measure with basin area (km^2). For variables assessed via multiple visits (such as sediment deposition and macroinvertebrate recolonization), analyses were randomized by time increment blocks and the repeated measures nature of the data was specified in the model. Data were checked for normality by visually inspecting normal probability plots and using Shapiro-Wilk tests (Zar 1999). Where data were deemed not normal, $\log_{10}$-transformations were performed except for proportional

variables bounded between 0 and 1 (i.e. available volume filled by deposited sediments and macroinvertebrate density relative to control baskets); these data were arcsine-square root transformed (Zar 1999). Tukey's post-hoc comparisons were conducted when sample sizes among treatment groups were unequal (i.e. for variables pertaining to flood water quality, where rural sites were underrepresented) to determine if pairwise mean comparisons results corresponded with ANOVA models. All analyses were conducted using the GLM and MIXED procedures in SAS (SAS Institute 2003).

Results

Channel morphometry and sediment structure

No differences in channel morphometry were detected between physiographic and rural/urban groups. ANOVA models for watershed size-standardized $\log_{10}$-transformed bankfull height ($F_{3,16}$=0.7, p=0.5577), bankfull width ($F_{3,16}$=0.2, p=0.8847), $\log_{10}$-transformed cross section area ($F_{3,16}$=0.7, p=0.5885) and $\log_{10}$-transformed large woody debris abundance ($F_{3,16}$=2.3, p=0.1202) were not significant.

Benthic particle sizes did vary among treatment groups, but differences between urban and rural streams were detected only in the Piedmont (Fig. 29). Overall ANOVA models for all three assessed percentiles (the D_{50}, $F_{3,16}$=11.1, p=0.0004; D_{75}, $F_{3,16}$=12.7, p=0.0002; and D_{90}, $F_{3,16}$=12.0, p=0.0003) were significant. As expected, Piedmont particle sizes were significantly larger relative to the Coastal Plain. Urban Piedmont streams possessed significantly greater particle sizes compared to rural sites for two of the three size classes (the D_{50} and D_{75}) analyzed. However, Coastal Plain benthic sediment structure was uniform between urban and rural sites.

Sediment movement and deposition

Tracer particle movement scores varied among treatment groups (Fig. 30). Large particles moved downstream significantly more in the Coastal Plain relative to the Piedmont and in urban compared to rural streams. However, the increase in movement scores between rural and urban sites was homogeneous between physiographic provinces as the ANOVA model interaction term was not statistically significant.

Water quality during flood events varied among groups; however, statistical comparisons may have been compromised by the disparity in sample sizes between rural and urban sites (Table 21). Twelve samples were collected from rural sites compared to 39 from urban sites. Regardless of the sample size disparity, significant differences among water quality parameters were detected among groups for some variables. TSS concentrations did not significantly vary between provinces or urban and rural streams ($p>0.05$ for all three model terms), though values from urban sites tended to be higher. The urban/rural ($F=15.9$, $p=0.0003$) and interaction ($F=6.48$, $p=0.0146$) terms of the TDS model were significant but not the provincial term ($F=0.0$, $p>0.05$), suggesting that TDS concentrations were more impacted by ISC in Coastal Plain streams. Urban/rural class terms in the $\log_{10}$-transformed conductivity ($F=17.9$, $p=0.0001$) and $\log_{10}$-transformed chloride ($F=7.0$, $p=0.0113$) models were statistically significant, though the remaining terms were not statistically significant for either variable. However, post-hoc comparisons suggested that chloride concentrations and conductivity were significantly more elevated in urban streams of the Coastal Plain (Table 21).

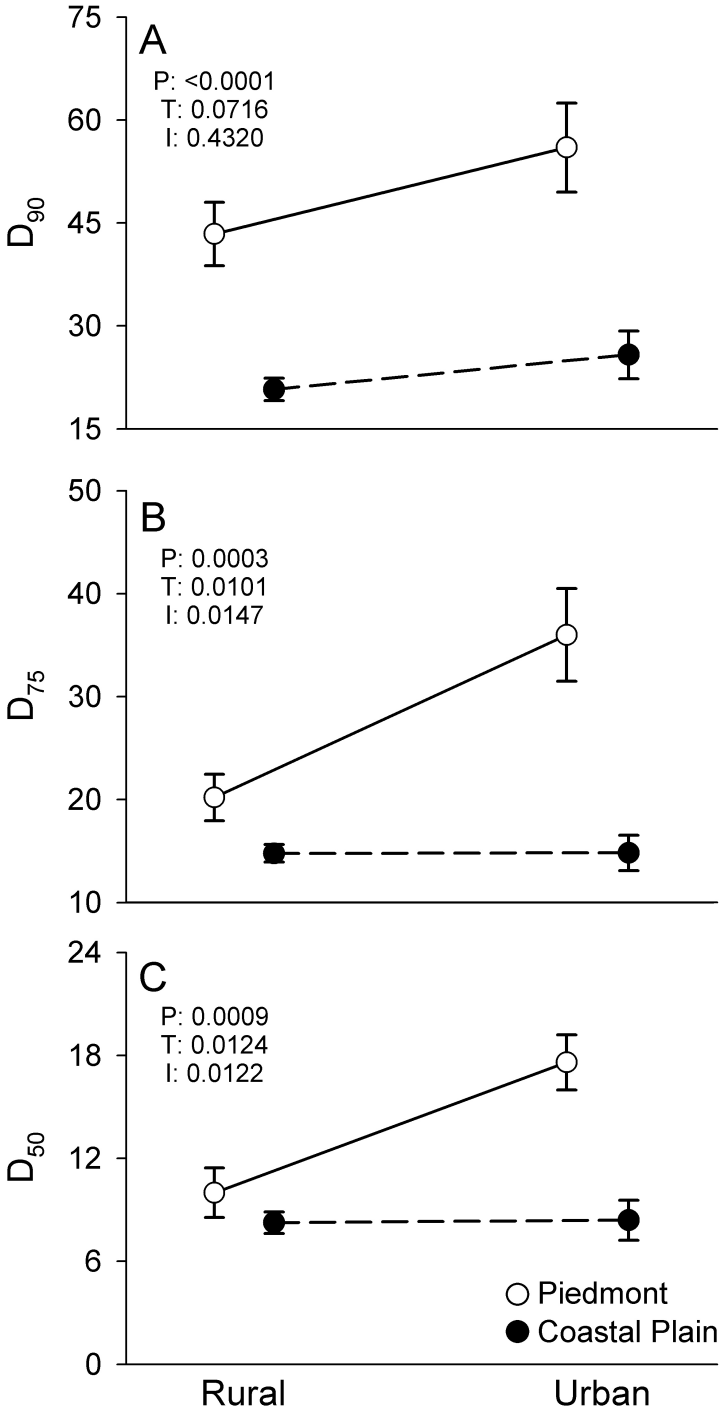

Figure 29. Benthic sediment regime characteristics among treatments. Shown are the D_{90} (A), D_{75} (B), and D_{50} (C) means ±1 standard error. p-values for ANOVA model terms are provided; P=province, T=treatment, I=province×treatment interaction.

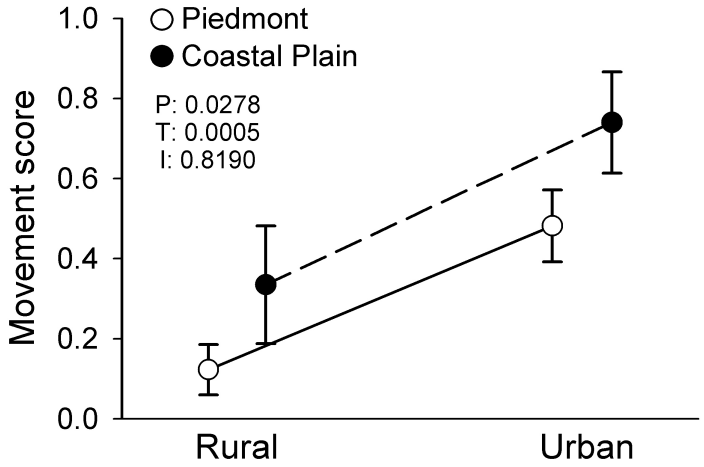

Figure 30. Mean (±1 standard error) sediment movement scores among treatments. p-values for ANOVA model terms are provided; P=province, T=treatment, I=province×treatment interaction.

Table 21. Floodwater chemistry differences among treatments. Values shown are means ±1 standard error. All variables were log_{10}-transformed for statistical comparisons. Letters denoting significant differences among means as indicated by Tukey post-hoc comparison tests are included only when at least one model term was significant.

	Rural sites		Urban sites	
Variable	Piedmont	Coastal Plain	Piedmont	Coastal Plain
Filled bottles	7	5	19	20
Total suspended solids (mg/L)	293.9±91.8	247.2±90.9	407.3±67.6	507.2±73.7
Total dissolved solids (mg/L $\times 10^{-1}$)	1.2 ± 0.2^{AB}	0.8 ± 0.1^{A}	1.5 ± 0.1^{B}	2.3 ± 0.4^{C}
Conductivity	146 ± 8.9^{AB}	78.5 ± 21.5^{A}	223.7 ± 23.3^{BC}	412 ± 115.6^{C}
Chloride (mg/L)	20.4 ± 3.2^{AB}	13.4 ± 2.9^{A}	34.7 ± 6.2^{AB}	71.5 ± 24.1^{B}

Significant differences among treatment groups were also detected in the amount and size of sediment passively collected by traps (Fig. 31). The total mass and proportion of available trap space filled by deposited sediments was significantly higher in Coastal Plain streams. Both variables were also significantly greater in

urban relative to rural streams, but only in the Piedmont. The median particle size of deposited sediments was significantly higher in Piedmont streams relative to the Coastal Plain and in urban settings; however, the interaction term for the median particle size model was not statistically significant.

Benthic macroinvertebrate colonization

Macroinvertebrates recolonized disturbed patches of sediment at varying rates between physiographic provinces and rural and urban streams (Fig. 32). Colonization rates based on taxonomic Bray-Curtis similarity relative to the control baskets were significantly higher in rural streams relative to urban streams, though significant differences were not detected between physiographic provinces. Though the overall density of organisms in control cages was about 50% higher in (rural) Piedmont streams, the differences were not statistically significant ($F_{3,16}$=2.0, $p>0.05$ in the three-term ANOVA model). Both physiographic province and the urban/rural class model terms were statistically significant in the macroinvertebrate density model. Treatment basket densities relative to the control baskets rose significantly faster in the Coastal Plain and in rural streams. Mean rural Coastal Plain macroinvertebrate densities were nearly 50% higher in the 24-day treatment baskets relative to the corresponding control, while densities in rural Piedmont streams remained about 50% lower than control patches after 24 days. Province-specific differences in recolonization as measured by density were also detected in urban streams, though the disparity was not as pronounced as observed in rural sites.

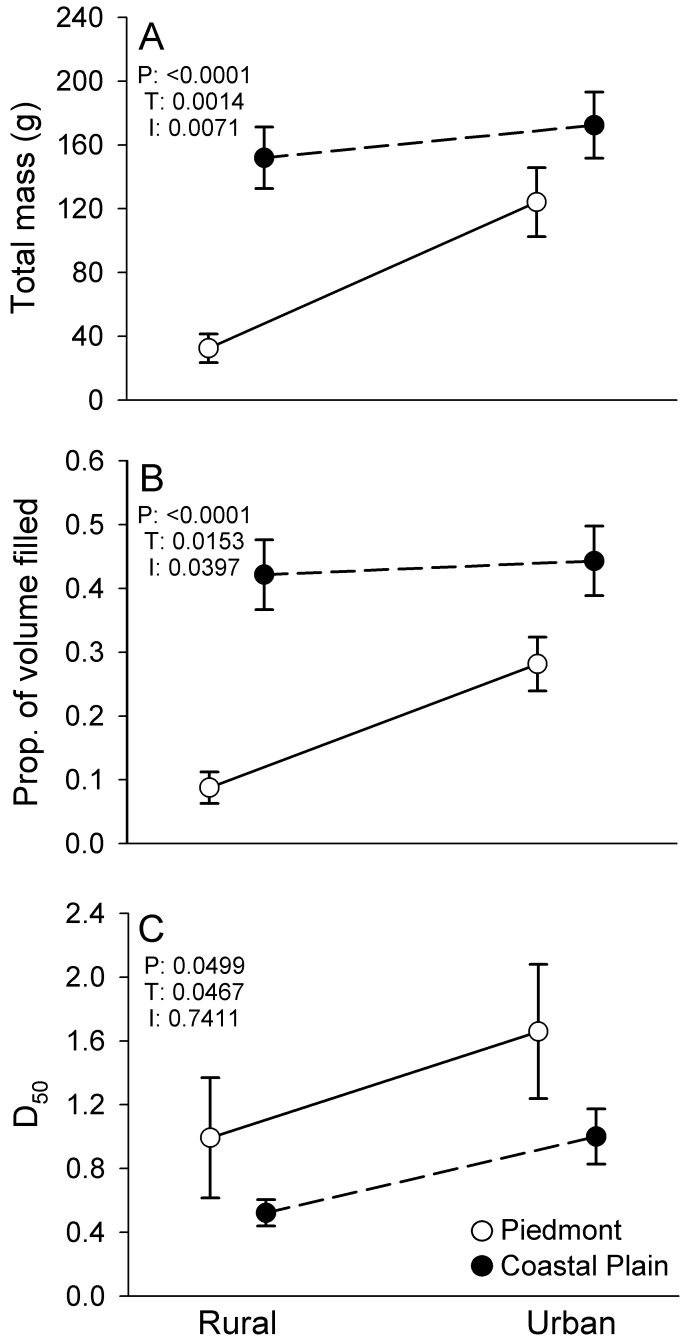

Figure 31. Mean (±1 standard error) mass (A), proportion of available volume filled (B), and median particle size (D_{50}; C) of sediments collected by passive *in situ* sediment traps among treatments. Total mass was $\log_{10}$-transformed and the proportion of available volume filled was arcsine-square root transformed prior to statistical comparisons.

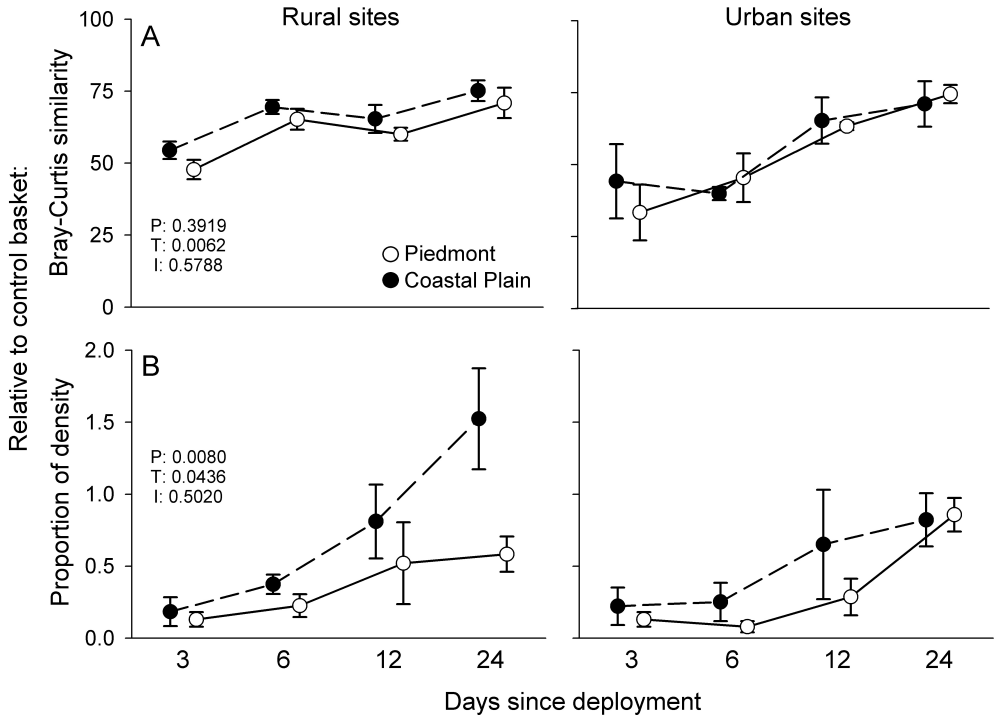

Figure 32. Benthic macroinvertebrate community colonization dynamics among treatments. Shown are mean Bray-Curtis similarity scores based on taxonomic presence/absence data (A) and mean density (B) relative to site-specific control baskets. Relative density was arcsine-square root transformed prior to statistical comparisons; error bars represent ±1 standard error. p-values for ANOVA model terms are provided; P=province, T=treatment, I=province×treatment interaction.

Discussion

As hypothesized, ISC-induced geomorphic degradation was more severe in Piedmont streams relative to those in the Coastal Plain. The interregional disparity was particularly acute in variables associated with sediment structure, stability, and large particle movement. Though benthic sediments were more unstable and prone to transport in rural Coastal Plain streams, sediment deposition and particle size was significantly elevated in urban relative to rural Piedmont sites while no such differences were detected in the Coastal Plain. Furthermore, though the increase in D_{75} and D_{90} particle movement between rural and urban sites was uniform between

provinces (Fig. 30), the corresponding particle sizes were much greater in the Piedmont and particularly urban Piedmont sites (Fig. 29). Thus when both particle movements and sizes are simultaneously considered, the disparity in large particle transport ability between rural and urban sites was substantially greater in the Piedmont.

Such results contribute to related work suggesting that streams with fine sediments in watersheds of low topographic relief are inherently less prone to geomorphic change in urban settings. Low gradient, sand/silt bottom streams in Oklahoma (Kang and Marston 2006) and Georgia (Riley 2009) exhibited neither signs of channel enlargement nor changes in threshold grain size (particle size assumed to be at the threshold of motion; Kang and Marston 2006 only) in urban versus rural settings; though Hardison et al. (2009) reported heighted channel incision in urban Coastal Plain streams. One reason why sediment structure regime change does not occur in the Coastal Plain may pertain to available streambed material; the large particles that dominate urbanized streams in other systems are simply not present in Coastal Plain channels. Furthermore, riparian wetlands, which tend to be more extensive in lowland ecosystems, may mitigate the hydrologic effects of urbanization (Burns et al. 2005, Riley 2009) thereby potentially reducing the impact on geomorphic and physicochemical properties. Regardless of the mechanism, biotic resiliency to urban land cover appears to be consistently greater in low gradient streams as well (Snyder et al. 2003, Utz et al. 2009), perhaps partially due to a relative absence of benthic habitat alteration.

Macroinvertebrate recolonization of disturbed habitat also occurred more rapidly in Coastal Plain streams despite the unstable sediment regime. In fact, macroinvertebrate densities in treatment baskets well exceeded those of controls after 24 days. Such a trend may have resulted from a relative lack of sand and silt between interstitial spaces in treatment baskets, as there was a low occurrence of sediment-transporting flood events during the experiment (Fig. 28). Regardless, Coastal Plain benthic biota appear to be relatively better dispersers and more opportunistic colonizers of hyporheic habitat. Thus the relative lack of geomorphic impact coupled with heightened habitat colonization ability in Coastal Plain streams may confer biotic resilience in urbanized settings.

Though the macroinvertebrate colonization disparity among treatments may seem to contradict findings in related studies, the spatial scale and likelihood of local adaptation must be considered when interpreting such results. Macroinvertebrate recolonization following disturbance has been reported to be facilitated in stable, large particle streambeds relative to those composed of finer particles (Cobb et al. 1992, Nislow 2002, Imbert et al. 2005). Yet all of the aforementioned studies were conducted within a small spatial scale in watersheds with uniform geoclimatic settings. In contrast, organisms inhabiting separate ecoregions (as in the Coastal Plain and Piedmont) are likely distinctly adapted to local disturbance regimes (Mackay 1992). Thus organisms in Coastal Plain streams recolonizing depauperate habitat patches more rapidly likely reflects local adaptation to the naturally unstable hyporheic zone.

The absence of differences in channel morphometry among treatment groups contrasts the majority of observed trends in related studies. Though stream channels in hydrogeomorphic settings similar to the Coastal Plain may not typically enlarge as a consequence of urbanization, those of the Piedmont consistently exhibit widening and/or incision in urban settings (Pizzuto et al. 2000, Allmendinger et al. 2007, Colosimo and Wilcock 2007). Furthermore, Coastal Plain streams are expected to possess naturally smaller bankfull widths and heights per unit of watershed area (Johnson and Fecko 2008). Why I did not detect similar differences in sites between rural and urban settings or physiographic provinces remains unclear, however, one potential explanation may involve the spatial scale of the study. Site locations were separated by distances over ~100km and encompassed a range of channel slopes (Fig. 27, Table 20). Therefore, the likelihood that stream morphometry varied partially due to local nuances in landform is considerable.

A number of factors not addressed in my approach should be recognized when interpreting the results. The structural arrangement and direct connectivity of ISC to stream channels was not considered though such information typically proves pertinent when deducing impact in urban streams (Booth and Jackson 1997, Walsh et al. 2009). However, floodwater chemical analyses suggested that connectivity may have been greater in the selected Coastal Plain urban streams, where a relative absence of geomorphic impact was observed. Sites in the Coastal Plain were only selected if streambeds were dominated by relatively large particles (cobble, gravel and sand). Yet many Coastal Plain streams possess sediment structures composed exclusively of sand and/or finer materials such as silt and clay. Whether or not more

or less impact would have been observed as a consequence of urbanization in streams with relatively fine sediments remains unclear. Though microclimatic differences among sites may have resulted in variable disturbance regimes, the fall and winter period was specifically selected to avoid intense localized storm events that most often occur during summer. The proportion of bottles filled among treatments suggests that precipitation variability was approximately equal across the study region. I simulated habitat disturbance to measure macroinvertebrate recolonization in place of observing dispersal following an actual storm. Thus the behavior of benthos following whole stream-scale disturbance may differ from what I reported, particularly in potentially critical habitats associated with organic debris such as log jams (Palmer et al. 1996).

Despite an absence of morphometric variability in channels among treatments, the majority of my results confirm a holistic disparity in stream ecosystem-scale responses to urbanization between the Coastal Plain and Piedmont. In addition to the differences in biotic sensitivity between these ecoregions, physiochemical baseline conditions and degradation along urban gradients varies as well. Rural Coastal Plain streams experience fewer flood events that are longer in duration and smaller in magnitude, yet each of these flow regime attributes changes significantly more along ISC gradients relative to streams in the Piedmont (Utz et al. *In review*). Conversely, thermal impact along ISC gradients is significantly greater in naturally cooler Piedmont streams. Such trends, along with the observed differences in geomorphic degradation, demonstrate that ecosystems may exhibit comprehensively unique responses to landscape stressors among regions.

Given the high likelihood that urbanization induces disparate degrees of ecosystem degradation in streams among ecoregions elsewhere, landscape-scale watershed management decisions should consider geoclimatic context in order to prove effective. Variability in hydrologic (Poff et al. 2006), chemical (Sprague and Nowell 2008), and habitat (Short et al. 2005) alteration caused by urbanization has been shown to differ among ecoregions other than the Coastal Plain and Piedmont; corresponding inequality in geomorphic responses also appears to be consistent. Yet generalities such as the assertion that stream ecosystem degradation accelerates near 10-15% watershed ISC (reviewed by Schueler et al. 2009) persist in and are often times assumed to apply ubiquitously. Comparative interregional approaches to landscape stressors and their effects on streams increasingly suggest that these concepts are vastly oversimplified: degradation intensity is context-dependent and certain environmental parameters may not respond in a uniform manner among stream forms. Further ecoregion-scale deduction of variability in environmental degradation is warranted in light of the rapidly increasing proportion of streams degraded by ISC (Theobald et al. 2009) and consequential loss of resources.

CHAPTER VII

CONCLUSION

My findings demonstrate substantial interregional heterogeneity in the extent of stream ecosystem degradation and associated decline in biodiversity along gradients of watershed urbanization. Streams in the Piedmont exhibited greater geomorphic and thermal impact as a consequence of urban development relative to those in the Coastal Plain. Furthermore, though hydrologic adjustment pertaining to the frequency, magnitude and duration of flood events along impervious surface cover (ISC) gradients was relatively greater in the Coastal Plain, Piedmont streams inherently possess flow regimes more prone to moderate flooding in rural watersheds. Therefore, physical disturbances associated with spates are more frequent and severe in the Piedmont until about 15% riparian- or watershed-scale ISC. The apparent effects of such differential abiotic impact between provinces on biotic responses are considerable. Sensitive fish and macroinvertebrate taxa are typically extirpated at lower levels of urbanization in the Piedmont, and taxa shared between provinces are more urbanization-tolerant in the Coastal Plain. A summary of all comparative ecosystem responses to urbanization between provinces is provided in Table 22.

Unfortunately, directly linking the specific abiotic mechanisms behind the disparate patterns in biological responses to urbanization remains impossible, yet my findings may be used to generate hypotheses to do so. For instance, lotic organisms are sensitive to episodic or prolonged elevated water temperatures (Caissie 2006), and the pronounced thermal shifts in urban Piedmont streams may be the primary factor inducing heightened intolerance to urbanization. Alternatively, the disproportionately

extensive benthic habitat degradation in the Piedmont may enhance biotic sensitivity to urban cover in that province. Such assertions using my results alone, however, are speculative and require direct observational or experimental approaches to adequately assess their validity. A single abiotic mechanism that causes the disparity in biotic sensitivity between provinces may not exist. Considering the diversity of sensitive fish and invertebrate taxa that consistently exhibit greater tolerance to urbanization in the Coastal Plain, the abiotic factors driving such trends may be multivariate and interactive.

Some attributes of my dissertation research involve inherent problems commonly associated with landscape-scale stream ecology and others unique to my project. Multiple landscape stressors may simultaneously affect streams (King et al. 2005), and most watersheds in the Mid-Atlantic possess a mix of urban and agricultural areas. For analyses such as those pertaining to hydrologic impact, agricultural land cover was not considered as an independent variable (though many streams exhibit negligible hydrologic responses to agriculture, Poff et al. 2006). In other dissertation components, highly agricultural watersheds were omitted but those used to model ecosystem responses possessed some agriculture. Thus some findings reported in this dissertation may have been affected in part by landscape stressors not included as independent variables. All dissertation analyses involved a space-for-time substitution. Rather than monitoring ecosystem degradation as watersheds urbanized, groups of sites at various states of urban development were assessed to model change over time. Another approach would be to explore environmental change in paired

Table 22. Summary of comparative ecosystem responses to gradients of urbanization between the Coastal Plain and Piedmont ecoregions of the eastern United States.

Variable	Qualitative differences in response	Notes and caveats
Flood hydrology	Frequency, magnitude and duration all more altered in Coastal Plain.	Despite greater impact along ISC gradient, disturbances are generally more frequent and severe in Piedmont until about 20% ISC.
Low flow event hydrology	No effect along ISC gradient detected in either province.	Roy et al. (2005) detected an increase in low flow event duration in Georgia Piedmont streams.
Temperature regime	Mean, maximum, and temperature surge duration more impacted in Piedmont	Only summer temperatures were tested; comparative effects during other seasons remain unknown.
Water quality	Majority of tested variables shift along ISC gradient uniformly between provinces; exceptions include total phosphorus and chlorophyll-a.	Differences in water quality during high flow events between provinces remain unknown. Potential differential impact on concentrations of toxins such as heavy metals, pesticides and herbicides not tested.
Benthic sediment structure	Shift towards larger particle sizes in Piedmont streams; no noticeable change in the Coastal Plain.	Effects of urbanization on Coastal Plain streams with benthic sediments dominated by sand, silt and clay remain unknown.
Sediment deposition and movement	Increase in sediment deposition along ISC gradient detected only in Piedmont, larger particles more readily transported in Piedmont.	Coastal Plain benthic sediments are inherently less stable; as a result, benthic organisms may be more opportunistic colonizers of disturbed habitat.
Channel morphology	No differences between urban/rural streams detected in either province.	Majority of related studies detect shifts following urbanization and differences between provinces.
Biota	Sensitive species extirpated at relatively lower levels of ISC in Piedmont streams.	Province-specific differences in biotic sensitivity for organisms other than fish and macroinvertebrates (such as amphibians) remains unexplored.

urban Coastal Plain and Piedmont watersheds as watershed evolved from rural to urban states to determine if results from such an approach agreed with overall findings. Finally, including more than two physiographic provinces in comparative environmental impact in urban streams might have strengthened assertions drawn from most of my dissertation components.

Regardless of the above uncertainties, my results concur with related work in identifying landform features that may confer ecosystem resiliency to urbanization in streams. For instance, Burns et al. (2005) demonstrated the ability of natural riparian wetlands to mitigate the hydrologic impact induced by urbanization in streams of the Croton River basin of upstate New York. By comparison, invertebrate communities inhabiting Maryland watersheds characterized by extensive wetland cover were the most resistant to urbanization, and Coastal Plain catchments in general tend to support more wetlands relative to the Piedmont. Snyder et al. (2003) concluded that fish communities in streams with the steepest gradients among their sites were most susceptible to environmental degradation induced by urbanization. Similarly, Coastal Plain streams possess gentler channel slopes and topographic gradients relative to the Piedmont. Both Kang and Marston (2006) and Riley (2009) observed a lack of geomorphic impact caused by urban development in watersheds with low channel gradients and unconsolidated sediments in place of bedrock. Therefore, streams draining watersheds with low topographic relief, extensive wetland cover and geologic attributes that promote groundwater seepage may prove relatively resilient to urban development in other locales as well.

Such results may be directly applied when implementing watershed management decisions. For instance, many government entities actively promote or enforce land use policies meant to prevent stream ecosystem degradation, including ISC limits within conservation priority catchments (WDNR 2000, MDNR 2005, Roy et al. 2008). My results suggest that the efficacy of such actions may vary among regions. In the Mid-Atlantic United States, an ISC limit may need to set be relatively lower for Piedmont watersheds compared to those in the Coastal Plain to preserve the same degree of biodiversity. Within-region watershed heterogeneity will also likely affect the utility of an ISC limit, as streams with abundant riparian wetlands and low slopes appear to require less protection relative to those in upland areas. A sizable number of restoration projects involve riparian plantings meant to eventually shade channels and consequentially maintain lower water temperatures (Hassett et al. 2005). These thermal mitigation projects may prove more valuable in the Piedmont where streams are cooler and simultaneously more impacted by urban development.

Many mitigation strategies prioritize disconnecting hydrologic linkages between ISC areas and stream channels (Roy et al. 2008), as hydrologic regime shift is considered the primary cause of ecosystem integrity decline in urban watersheds (Booth 2005, Roy et al. 2005, Degasperi 2009). My dissertation results also suggest that managing hydrologic degradation in urbanized streams is principally important. The Coastal Plain hydrogeologic setting and characteristic flood regime appears to buffer aquatic organisms from the effects of urban development relative to those of the Piedmont (though Coastal Plain streams are still degraded by the implementation of ISC). While multiple differences in abiotic environmental impact were detected

between provinces, nearly all are directly or indirectly related to flow regime. For instance, the armor layer observed in urbanized Piedmont streams developed due to the increased small particle transport induced by ISC-related floods. In another example, the elevation of mean and maximum summer temperatures in urban Piedmont streams was likely partially driven by the delivery of ISC-heated water during spates. Therefore, my findings strongly advocate for restoration and conservation strategies that emphasize the retention or return of natural flow regimes to impacted watersheds. Examples of such practices in urban catchments include the use of rain gardens, permable pavement, rain barrels, and green roofs (Roy et al. 2008). The majority of my results do not, however, suggest that habitat restoration efforts alone (which are prioritized over flow regime restoration efforts in the United States, Hassett et al. 2005) will restore biodiversity in urbanized streams.

My findings strongly advocate for ecoregion-based approaches and recognition of heterogeneity when quantifying all forms of environmental degradation caused by landscape stressors in streams. Though biologists have long recognized the significance of geoclimatic boundaries in delineating the distributions of species and communities (Stoddard 2004), many have assumed that categorical classes of landscape stressors cause relatively homogeneous change in streams among regions. Interregional comparative approaches consistently demonstrate heterogeneity in ecosystem responses to landscape stressors (i.e. Liu et al. 2000, Poff et al. 2006, Sprague and Nowell 2008, this dissertation). Even basic biotic responses to landscape stressors may prove counterintuitive; for instance, frog assemblages of the Australian Blue Mountains are more intact in urban relative to rural streams because elevated

chloride concentrations reduce the severity of chytridiomycosis infections (Lane and Burgin 2008). Thus broad assertions pertaining to the effects of landscape stressors on streams, such as the concept of rapid ecosystem degradation once watershed ISC reaches 10% (Schueler et al. 2009), are likely to prove highly inconsistent. Future efforts to quantify, prevent, or mitigate the effects of landscape stressors on stream ecosystems must acknowledge the geoclimatic diversity of watersheds and how this critical factor mediates environmental degradation.

Due to the idiosyncratic nature of landscape-scale stream ecosystem degradation, my findings should be applied with caution. I presented landscape stressor thresholds of minimum impact and maximum tolerance for aquatic taxa and communities. Watershed managers should not consider these values static or absolute. For instance, allowing catchment development up to a T_{95} does not ensure that the corresponding sensitive organism or community will persist; in fact, 95% of a taxon's occurrence (or abundance) is lost by the T_{95}. Thresholds such as the D_1 and T_{95} will likely vary among sites due to local environmental and hydrogeologic features. Further, stressors unrelated to land use such as climate change or species introductions may cause these ecological thresholds to shift over time (Groffman et al. 2006). While Coastal Plain stream ecosystems appear to be relatively more resistant to degradation induced by urbanization, they are far from invulnerable. Ecologically intact Coastal Plain watersheds with high levels of biodiversity, such as Nassawango and Mattawoman Creeks in Maryland, may be readily impacted by even moderate levels of development as demonstrated by the uniformly low taxon-specific- and community-scale D_1 values. Finally, my dissertation focused primarily on landscape-scale

relationships with stream biodiversity, but these findings may not apply to management efforts pertaining to other ecosystem services. For example, most fish and invertebrate taxa in Maryland appear to be highly tolerant of agricultural development (Utz et al. 2009, Utz et al. in press). Yet some watershed managers in the Chesapeake Bay are primarily concerned with nitrogen loss from catchments that contribute to estuarine eutrophication, and agricultural areas export far greater levels of total nitrogen compared to forest or urban land uses (Boesch et al. 2001, King et al. 2005).

A number of novel research questions relating to my dissertation remain. For instance, if trends such as those presented in my dissertation are consistently detected, may we collectively produce a predictive framework of stream ecosystem sensitivity to specific landscape stressors across all ecoregions? The concordance of my results with a handful of related efforts suggests that this may be possible, but substantially more work will be necessary to produce such a tool. Do the primary physicochemical factors inducing biotic integrity decline in urban streams vary among ecoregions? Because the severity and/or nature of physicochemical responses to landscape stressors vary among geoclimatic settings, the abiotic parameters most responsible for biodiversity loss due to land use change may prove diverse as well. Determining whether or not this is the case will require experimental and/or direct observational work with sensitive aquatic organisms. Can we exploit natural landscape features to limit the impact of urban development on streams? Recent assessments have demonstrated that simply leaving riparian zones intact does not minimize impact (Roy et al. 2007, Walsh et al. 2007). However, my results suggest that restricting

urban development to areas with the gentlest topographic gradients and allowing natural wetlands to mitigate hydrologic degradation may prevent degradation in streams. Investigating all such inquiries may eventually allow landscape managers to effectively conserve stream ecosystem resources in the face of rapidly expanding urban development.

APPENDICES

Appendix A. Catalog of invertebrate taxa responses to catchment urbanization in Maryland. Taxa with an asterisk (*) displayed a significantly positive relationship with urban land. For taxa neutrally or positively distributed with urban land, the T_{95} value represents the maximum catchment urbanization where the taxon was collected. pH represents the level below which streams were not included for analysis.

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
Coastal Plain									
	Enopla								
		Hoplonemertea							
			Tetrastemmatidae						
				*Prostoma**	6.14	62	0.0013	-	88.1
	Gastropoda								
		Basommatophora							
			Lymnaeidae						
				Pseudosuccinea	6.02	38	0.5785	-	91.1
				*Stagnicola**	6.09	26	0.0455	-	88.1
			Physidae						
				Physella	6.24	173	0.8350	-	94.1
			Planorbidae						
				Menetus	5.82	54	0.0524	-	84.1
	Insecta								
		Coleoptera							
			Dryopidae						
				Helichus	6.29	33	0.0290	7.0	58.1
			Dytiscidae						
				Agabus	4.46	31	0.4418	-	82.1
				Hydroporus	4.86	111	0.3289	-	91.1
			Elmidae						
				Ancyronyx	6.02	64	0.9564	-	93.1
				Dubiraphia	5.93	103	0.0263	1.2	58.1
				Macronychus	6.50	41	<0.0001	2.5	56.1
				Optioservus	6.48	63	0.0117	5.9	56.1
				Oulimnius	6.16	96	0.0173	4.7	48.7
				Stenelmis	6.28	127	0.0075	28.5	57.8
			Gyrinidae						
				Dineutus	5.97	51	0.0746	-	80.1
			Haliplidae						
				Peltodytes	5.30	30	0.3409	-	59.9
			Ptilodactylidae						
				Anchytarsus	5.93	43	<0.0001	2.9	28.2
		Collembola							
			Isotomidae						
				*Isotomurus**	5.01	45	0.0001	-	88.1
		Diptera							

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Ceratopogonidae						
				Bezzia	5.80	29	<0.0001	7.6	18.1
				Ceratopogon	5.60	42	0.1256	-	87.8
				Culicoides	4.94	26	0.5785	-	59.3
				Probezzia	5.90	48	0.0117	3.2	46.4
			Chironomidae						
				Ablabesmyia	5.30	125	0.1949	-	88.1
				Apsectrotanypus	5.17	42	<0.0001	1.0	18.4
				Brillia	6.23	71	0.5343	-	77.4
				Chaetocladius	5.40	34	<0.0001	1.0	22.8
				Chironomini	4.55	49	0.8161	-	94.1
				Chironomus	4.55	42	0.7111	-	91.9
				Clinotanypus	5.30	49	<0.0001	1.0	4.6
				Conchapelopia	5.91	256	0.8241	-	94.1
				Corynoneura	5.34	146	0.0052	1.2	26.4
				*Cricotopus**	6.12	142	<0.0001	-	93.1
				Cricotopus/Orthoclad	6.07	308	0.4772	-	93.1
				Cryptochironomus	6.10	55	0.1266	-	91.9
				Diamesa	6.69	28	<0.0001	55.6	57.8
				Dicrotendipes	5.82	84	0.1531	-	94.1
				Diplocladius	5.45	92	0.0033	8.3	49.4
				Endochironomus	5.36	28	0.7619	-	80.2
				Eukiefferiella	6.03	155	0.6288	-	88.9
				Heterotrissocladius	4.94	42	<0.0001	20.5	57.2
				Hydrobaenus	5.50	143	0.2512	-	84.4
				Labrundinia	6.08	31	<0.0001	1.0	32.5
				*Limnophyes**	4.76	35	<0.0001	-	84.4
				*Meropelopia**	5.66	79	0.0006	-	91.1
				Micropsectra	6.00	121	0.1760	-	84.4
				Microtendipes	6.12	93	0.0039	3.2	26.4
				Nanocladius	5.69	91	0.4047	-	94.1
				Natarsia	5.47	26	0.2255	-	79.5
				Orthocladius	6.03	237	0.3668	-	94.1
				Parametriocnemus	6.10	310	0.0467	9.7	56.5
				Paraphaenocladius	5.49	60	0.0674	-	79.5
				Paratanytarsus	6.19	108	0.3663	-	91.1
				Paratendipes	6.30	31	<0.0001	2.0	58.1
				Phaenopsectra	5.66	91	0.3523	-	94.1
				Polypedilum	5.68	392	0.4166	-	93.1
				Procladius	5.44	52	0.0642	-	87.8
				Pseudorthocladius	4.89	29	0.4418	-	63.5

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				*Rheocricotopus**	5.79	203	0.3136	-	88.1
				Rheotanytarsus	6.17	194	0.1035	-	77.8
				Stempellinella	6.43	34	<0.0001	2.3	13.8
				*Stenochironomus**	5.92	51	<0.0001	-	80.1
				Symposiocladius	5.85	64	0.9085	-	91.1
				Tanytarsus	5.91	219	0.0943	-	93.1
				Thienemanniella	6.15	125	0.0869	-	82.9
				Thienemannimyia	5.45	46	0.3409	-	84.1
				Tribelos	4.37	81	0.6229	-	91.1
				Trissopelopia	5.90	65	0.0554	-	82.0
				Tvetenia	5.46	104	0.0114	5.4	48.7
				Xylotopus	5.98	28	0.4418	-	84.1
				Zavrelimyia	5.44	183	0.9511	-	93.1
			Empididae						
				Chelifera	6.32	44	0.1256	-	83.7
				Hemerodromia	6.32	121	0.7389	-	88.9
			Simulidae						
				Prosimulium	6.00	245	0.0048	6.1	34.2
				Simulium	5.90	193	<0.0001	1.2	48.9
				Stegopterna	5.11	271	0.0023	3.8	46.2
			Tabanidae						
				Chrysops	5.01	66	0.0321	3.6	56.1
			Tipulidae						
				Dicranota	5.74	38	<0.0001	6.2	26.1
				Hexatoma	5.63	87	<0.0001	7.0	37.8
				Ormosia	5.30	27	0.4047	-	78.2
				Pseudolimnophila	5.64	95	0.0387	6.4	56.5
				Tipula	6.10	181	0.1792	-	91.1
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	26	<0.0001	7.7	34.5
			Baetidae						
				Acentrella	6.52	26	0.0690	-	77.7
				Acerpenna	6.19	168	0.0020	2.5	39.3
			Caenidae						
				Caenis	5.87	38	0.1699	-	68.3
			Ephemerellidae						
				Ephemerella	6.47	122	0.0045	3.8	46.4
				Eurylophella	6.09	134	0.0391	7.1	59.8
			Heptageniidae						
				Stenonema	6.35	195	0.0039	2.4	48.7

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Leptophlebidae						
				Leptophlebia	5.34	93	<0.0001	2.9	28.2
				Paraleptophlebia	6.43	29	0.0956	-	90.8
		Megaloptera							
			Corydalidae						
				Nigronia	5.63	89	<0.0001	10.3	51.5
			Sialidae						
				Sialis	4.91	41	0.0161	10.5	58.1
		Odonata							
			Aeshnidae						
				Boyeria	5.85	83	0.7324	-	91.1
			Calopterygidae						
				Calopteryx	6.00	159	0.9822	-	91.1
			Coenagrionidae						
				*Argia**	6.08	46	<0.0001	-	96.7
			Cordulegastridae						
				Cordulegaster	5.49	48	0.0239	6.1	46.2
		Plecoptera							
			Capniidae						
				Allocapnia	5.93	33	<0.0001	3.5	16.9
			Leuctridae						
				Leuctra	5.03	55	<0.0001	3.6	47.2
			Nemouridae						
				Amphinemura	6.07	150	0.0023	6.5	47.0
				Prostoia	6.04	113	0.0098	6.1	45.0
			Perlidae						
				Eccoptura	5.90	61	<0.0001	3.6	26.1
			Perlodidae						
				Clioperla	6.07	46	<0.0001	5.6	19.8
				Isoperla	6.27	135	0.0024	4.1	45.7
			Taeniopterygidae						
				Strophopteryx	6.42	39	<0.0001	13.4	34.5
				Taeniopteryx	6.37	27	0.0690	-	91.1
		Trichoptera							
			Hydropsychidae						
				Cheumatopsyche	6.31	277	0.2788	-	91.9
				Diplectrona	5.86	93	<0.0001	6.6	39.8
				Hydropsyche	6.47	160	0.7976	-	93.1
			Leptoceridae						
				Oecetis	5.70	25	<0.0001	1.2	45.6

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Triaenodes	5.17	39	0.5785	-	80.2
			Limnephilidae						
				Ironoquia	4.93	110	0.0232	3.1	53.3
				Pycnopsyche	5.60	103	<0.0001	4.9	26.1
			Philopotamidae						
				Chimarra	6.60	29	<0.0001	2.4	46.3
			Phryganeidae						
				Ptilostomis	5.32	51	0.6637	-	72.5
			Polycentropodidae						
				Polycentropus	5.11	77	0.0045	1.2	39.8
			Psychomyiidae						
				Lype	6.00	82	<0.0001	3.5	31.5
			Uenoidae						
				Neophylax	6.26	100	<0.0001	6.1	56.3
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				Crangonyx	4.82	233	0.2266	-	84.4
			Gammaridae						
				Gammarus	6.28	200	0.0103	3.9	36.2
				*Stygonectes**	4.92	25	0.0137	-	93.1
			Hyalellidae						
				Hyalella	5.93	43	0.4047	-	80.2
		Isopoda							
			Asellidae						
				Caecidotea	4.86	376	0.0087	1.2	47.2
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae*		5.36	240	0.0230	-	96.7
		Tubificida							
			Enchytraeidae*		5.46	98	<0.0001	-	91.9
			Naididae		6.00	150	0.3373	-	94.1
			Tubificidae						
				*Limnodrilus**	5.79	70	<0.0001	-	94.1
	Plececypoda								
		Veneroida							
			Sphaeriidae						
				Pisidium	5.74	88	0.2021	-	93.1
				Sphaerium	5.95	66	0.0290	1.6	53.8
	Turbellaria								
		Tricladida							

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Planariidae						
				*Dugesia**	6.24	42	0.0016	-	93.1
Piedmont	Enopla								
		Hoplonemertea							
			Tetrastemmatidae						
				*Prostoma**	6.14	29	0.0088	-	76.1
	Gastropoda								
		Basommatophora							
			Physidae						
				*Physella**	6.24	63	0.0074	-	98.5
	Insecta								
		Coleoptera							
			Elmidae						
				Dubiraphia	5.93	50	0.0080	3.6	45.6
				Macronychus	6.50	33	0.0189	11.4	53.8
				Optioservus	6.48	329	0.0050	2.2	42.9
				Oulimnius	6.16	196	0.0050	4.6	41.6
				Stenelmis	6.28	207	0.6740	-	93.2
			Psephenidae						
				Psephenus	6.49	69	0.0046	7.0	43.4
			Ptilodactylidae						
				Anchytarsus	5.93	89	<0.0001	2.7	36.8
		Diptera							
			Ceratopogonidae						
				Ceratopogon	5.60	28	0.4418	-	61.1
				Probezzia	5.90	52	0.0077	0.5	41.6
			Chironomidae						
				Brillia	6.23	126	0.0659	-	76.5
				*Chaetocladius**	5.40	37	0.0018	-	74.0
				Conchapelopia	5.91	275	0.3825	-	89.8
				Corynoneura	5.34	150	0.0910	-	96.5
				*Cricotopus**	6.12	131	<0.0001	-	92.8
				Cricotopus/Orthocl	6.07	391	0.8771	-	93.0
				Cryptochironomus	6.10	31	0.0239	8.1	33.8
				Diamesa	6.69	301	0.7452	-	79.8
				*Dicrotendipes**	5.82	32	<0.0001	-	88.9
				*Diplocladius**	5.45	29	0.0001	-	82.2
				Eukiefferiella	6.03	280	0.3001	-	92.5
				Heterotrissocladius	4.94	27	0.0358	35.7	51.3
				Hydrobaenus	5.50	131	0.7796	-	76.1
				Meropelopia	5.66	59	0.1297	-	83.3

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Micropsectra	6.00	151	0.0041	1.6	37.6
				Microtendipes	6.12	132	0.0102	4.5	36.7
				Nanocladius	5.69	58	0.3409	-	88.9
				Orthocladius	6.03	357	0.9682	-	98.5
				Parakiefferiella	5.00	33	0.0202	3.5	42.9
				Parametriocnemus	6.10	512	0.0935	-	96.5
				Paraphaenocladius	5.49	45	0.3409	-	62.3
				*Paratanytarsus**	6.19	67	0.0001	-	88.9
				Polypedilum	5.68	241	0.5707	-	88.9
				*Rheocricotopus**	5.79	82	0.0314	-	81.5
				Rheotanytarsus	6.17	183	0.3687	-	85.4
				Stempellinella	6.43	40	<0.0001	0.9	13.6
				Stictochironomus	5.25	27	0.0358	7.8	44.5
				Symposiocladius	5.85	26	0.0518	-	96.5
				Sympotthastia	6.72	215	0.0923	-	82.5
				Tanytarsus	5.91	176	0.3136	-	88.9
				Thienemanniella	6.15	192	0.0039	7.9	53.2
				*Thienemannimyia**	5.45	60	<0.0001	-	96.5
				Trissopelopia	5.90	109	0.0402	9.7	30.8
				Tvetenia	5.46	182	0.6339	-	87.6
				Zavrelimyia	5.44	96	0.8607	-	87.6
			Empididae						
				Chelifera	6.32	74	0.1612	-	85.8
				Clinocera	6.70	180	0.0285	4.9	44.8
				Hemerodromia	6.32	170	0.1773	-	93.1
			Simulidae						
				Prosimulium	6.00	439	0.0020	3.5	22.1
				Simulium	5.90	217	0.7730	-	87.6
				Stegopterna	5.11	148	0.0290	8.9	43.1
			Tabanidae						
				Chrysops	5.01	31	0.0263	7.6	41.6
			Tipulidae						
				Antocha	6.66	295	0.8648	-	92.8
				Dicranota	5.74	84	0.0155	2.0	23.6
				Hexatoma	5.63	69	<0.0001	1.5	25.6
				Pseudolimnophila	5.64	75	0.0041	1.5	28.7
				Tipula	6.10	233	0.0895	-	93.1
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	149	0.0019	4.3	19.2
			Baetidae						

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Acerpenna	6.19	65	0.0048	3.6	16.6
				Baetis	6.58	70	0.0048	9.6	30.1
			Ephemerellidae						
				Drunella	6.86	30	<0.0001	1.5	5.8
				Ephemerella	6.47	436	0.0015	2.1	20.4
				Eurylophella	6.09	209	0.0119	4.5	42.9
				Serratella	6.86	86	<0.001	1.9	16.6
			Ephemeridae						
				Ephemera	6.91	28	<0.0001	1.5	9.0
			Heptageniidae						
				Epeorus	6.49	102	<0.0001	0.9	11.4
				Stenacron	6.47	42	0.0124	2.6	44.8
				Stenonema	6.35	377	0.0016	3.3	41.0
			Isonychiidae						
				Isonychia	6.98	148	<0.0001	2.2	13.4
			Leptophlebidae						
				Leptophlebia	5.34	32	0.0239	4.2	16.6
				Paraleptophlebia	6.43	124	<0.0001	1.3	14.1
		Megaloptera							
			Corydalidae						
				Corydalus	6.75	30	<0.0001	8.8	41.2
				Nigronia	5.63	102	0.0089	11.4	41.2
			Sialidae						
				Sialis	4.91	35	<0.0001	8.1	39.3
		Odonata							
			Calopterygidae						
				*Calopteryx**	6.00	40	<0.0001	-	76.5
		Plecoptera							
			Capniidae						
				Allocapnia	5.93	51	<0.0001	5.2	14.3
				Paracapnia	5.85	43	<0.0001	7.7	25.6
			Leuctridae						
				Leuctra	5.03	45	0.0124	1.0	31.7
			Nemouridae						
				Amphinemura	6.07	310	0.0019	1.7	26.7
				Prostoia	6.04	218	0.0025	2.7	20.3
			Perlidae						
				Acroneuria	6.52	77	0.0042	2.7	20.6
				Eccoptura	5.90	42	<0.0001	7.2	40.0
			Perlodidae						
				Isoperla	6.27	41	<0.0001	1.0	10.1

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Taeniopterygidae						
				Oemopteryx	6.19	26	0.0402	3.7	42.7
				Strophopteryx	6.42	90	<0.0001	2.7	13.4
		Trichoptera							
			Glossosomatidae						
				Glossosoma	6.41	42	<0.0001	1.6	31.4
			Hydropsychidae						
				Cheumatopsyche	6.31	478	0.2767	-	98.5
				Diplectrona	5.86	209	0.2871	-	96.5
				Hydropsyche	6.47	428	0.6777	-	98.5
			Limnephilidae						
				Pycnopsyche	5.60	51	0.0083	1.3	19.2
			Philopotamidae						
				Chimarra	6.60	161	0.0018	3.3	42.7
				Dolophilodes	5.77	50	<0.0001	11.4	20.6
			Polycentropodidae						
				Polycentropus	5.11	53	<0.0001	3.3	23.6
			Psychomyiidae						
				Lype	6.00	32	0.0263	2.0	17.6
			Rhyacophilidae						
				Rhyacophila	5.83	141	<0.0001	2.7	22.1
			Uenoidae						
				Neophylax	6.26	241	0.0024	3.5	30.5
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				*Crangonyx**	4.82	102	<0.0001	-	93.0
			Gammaridae						
				Gammarus	6.28	35	0.0173	35.7	48.6
		Isopoda							
			Asellidae						
				*Caecidotea**	4.86	38	<0.0001	-	89.8
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae*		5.36	154	<0.0001	-	98.5
		Tubificida							
			Enchytraeidae*		5.46	76	<0.0001	-	98.5
			Naididae		6.00	195	0.1916	-	92.5
	Plececypoda								
		Veneroida							
			Sphaeriidae						

Appendix A (continued).

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Sphaerium	5.95	25	0.5050	-	96.5
	Turbellaria								
		Tricladida							
			Planariidae						
				Dugesia	6.24	63	0.5785	-	89.8

Appendix B. Catalog of invertebrate taxa responses to catchment ISC in Maryland. Taxa with an asterisk (*) displayed a significantly positive relationship with ISC. For taxa neutrally or positively distributed with ISC, the T_{95} value represents the maximum catchment urbanization where the taxon was collected. pH represents the level below which streams were not included for analysis.

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
Coastal Plain									
	Enopla								
		Hoplonemertea							
			Tetrastemmatidae						
				*Prostoma**	6.14	62	0.0013	-	35.4
	Gastropoda								
		Basommatophora							
			Lymnaeidae						
				Pseudosuccinea	6.02	38	0.1385	-	35.4
				*Stagnicola**	6.09	26	0.0455	-	34.9
			Physidae						
				Physella	6.24	173	0.6769	-	43.1
			Planorbidae						
				Menetus	5.82	54	0.1699	-	42.3
	Insecta								
		Coleoptera							
			Dryopidae						
				Helichus	6.29	33	<0.0001	1.4	18.8
			Dytiscidae						
				Agabus	4.46	31	0.0727	-	37.5
				Hydroporus	4.86	111	0.0990	-	36.7
			Elmidae						
				Ancyronyx	6.02	64	0.9564	-	34.8
				Dubiraphia	5.93	103	0.0640	-	34.8
				Macronychus	6.50	41	<0.0001	1.1	17.8
				Optioservus	6.48	63	0.0117	5.1	21.7
				Oulimnius	6.16	96	0.0043	0.7	17.9
				Stenelmis	6.28	127	0.0441	9.2	22.6
			Gyrinidae						
				Dineutus	5.97	51	0.3136	-	38.0
			Haliplidae						
				Peltodytes	5.30	30	0.3409	-	20.8
			Ptilodactylidae						
				Anchytarsus	5.93	43	<0.0001	0.6	6.1
		Collembola							
			Isotomidae						
				Isotomurus	5.01	45	0.1531	-	35.4
		Diptera							

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Ceratopogonidae						
				Bezzia	5.80	29	<0.0001	1.4	3.3
				Ceratopogon	5.60	42	0.1256	-	33.6
				Culicoides	4.94	26	<0.0001	6.6	16.4
				Probezzia	5.90	48	0.0117	0.9	15.7
			Chironomidae						
				Ablabesmyia	5.30	125	0.9508	-	43.1
				Apsectrotanypus	5.17	42	<0.0001	0.2	4.2
				Brillia	6.23	71	0.9549	-	36.7
				Chaetocladius	5.40	34	<0.0001	1.2	4.1
				Chironomini	4.55	49	0.5874	-	38.0
				Chironomus	4.55	42	0.1949	-	36.9
				Clinotanypus	5.30	49	<0.0001	0.5	1.1
				Conchapelopia	5.91	256	0.9410	-	43.1
				Corynoneura	5.34	146	0.0022	0.6	9.0
				*Cricotopus**	6.12	142	<0.0001	-	43.1
				Cricotopus/Orthocl	6.07	308	0.4772	-	43.1
				*Cryptochironomus**	6.10	55	0.0263	-	42.3
				Diamesa	6.69	28	<0.0001	15.9	23.3
				Dicrotendipes	5.82	84	0.1531	-	34.8
				Diplocladius	5.45	92	0.0111	2.1	16.4
				Endochironomus	5.36	28	0.2255	-	34.8
				Eukiefferiella	6.03	155	0.4606	-	36.9
				Heterotrissocladius	4.94	42	0.0161	2.8	17.9
				Hydrobaenus	5.50	143	0.3819	-	37.5
				Labrundinia	6.08	31	<0.0001	0.4	11.7
				*Limnophyes**	4.76	35	<0.0001	-	37.5
				Meropelopia	5.66	79	0.1432	-	36.7
				Micropsectra	6.00	121	0.0923	-	34.9
				Microtendipes	6.12	93	<0.0001	0.6	9.0
				Nanocladius	5.69	91	0.4047	-	43.1
				Natarsia	5.47	26	0.2255	-	36.9
				Orthocladius	6.03	237	0.2772	-	41.0
				Parametriocnemus	6.10	310	0.0167	2.5	20.2
				Paraphaenocladius	5.49	60	0.0074	1.6	17.8
				Paratanytarsus	6.19	108	0.0518	-	34.8
				Paratendipes	6.30	31	<0.0001	0.8	18.8
				Phaenopsectra	5.66	91	0.8769	-	43.1
				Polypedilum	5.68	392	0.5946	-	43.1
				Procladius	5.44	52	0.0640	-	33.6
				Pseudorthocladius	4.89	29	<0.0001	6.1	18.0

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Rheocricotopus	5.79	203	0.4157	-	36.9
				Rheotanytarsus	6.17	194	0.0565	-	35.1
				Stempellinella	6.43	34	<0.0001	0.7	4.3
				*Stenochironomus**	5.92	51	0.0263	-	38.0
				Symposiocladius	5.85	64	0.6457	-	35.4
				Tanytarsus	5.91	219	0.0783	-	35.4
				Thienemanniella	6.15	125	0.0690	-	35.1
				Thienemannimyia	5.45	46	0.1531	-	42.3
				Tribelos	4.37	81	0.0903	-	42.3
				Trissopelopia	5.90	65	0.0087	0.5	20.0
				Tvetenia	5.46	104	0.0114	0.8	14.0
				Xylotopus	5.98	28	0.6081	-	42.3
				Zavrelimyia	5.44	183	0.8862	-	38.0
			Empididae						
				Chelifera	6.32	44	0.7870	-	35.4
				Hemerodromia	6.32	121	0.7389	-	43.1
			Simulidae						
				Prosimulium	6.00	245	0.0048	0.8	10.0
				Simulium	5.90	193	<0.0001	0.5	14.0
				Stegopterna	5.11	271	0.0023	1.2	13.1
			Tabanidae						
				Chrysops	5.01	66	0.1217	-	30.5
			Tipulidae						
				Dicranota	5.74	38	<0.0001	1.7	4.6
				Hexatoma	5.63	87	<0.0001	1.5	11.0
				Ormosia	5.30	27	0.5785	-	34.9
				Pseudolimnophila	5.64	95	0.0128	1.1	16.4
				Tipula	6.10	181	0.3977	-	41.0
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	26	<0.0001	0.8	10.3
			Baetidae						
				Acentrella	6.52	26	0.0690	-	30.2
				Acerpenna	6.19	168	<0.0001	0.6	11.4
			Caenidae						
				Caenis	5.87	38	0.1699	-	24.1
			Ephemerellidae						
				Ephemerella	6.47	122	0.0032	0.7	11.6
				Eurylophella	6.09	134	0.1531	-	34.8
			Heptageniidae						
				Stenonema	6.35	195	0.0039	0.6	15.9

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Leptophlebidae						
				Leptophlebia	5.34	93	<0.0001	0.7	6.9
				Paraleptophlebia	6.43	29	1.0000	-	31.2
		Megaloptera							
			Corydalidae						
				Nigronia	5.63	89	<0.0001	2.5	17.4
			Sialidae						
				Sialis	4.91	41	0.0161	3.8	18.8
		Odonata							
			Aeshnidae						
				Boyeria	5.85	83	0.4418	-	34.9
			Calopterygidae						
				Calopteryx	6.00	159	0.8404	-	43.1
			Coenagrionidae						
				*Argia**	6.08	46	<0.0001	-	54.3
			Cordulegastridae						
				Cordulegaster	5.49	48	0.0239	0.8	14.7
		Plecoptera							
			Capniidae						
				Allocapnia	5.93	33	<0.0001	0.5	5.1
			Leuctridae						
				Leuctra	5.03	55	<0.0001	1.5	10.6
			Nemouridae						
				Amphinemura	6.07	150	0.0058	1.2	15.0
				Prostoia	6.04	113	0.0098	1.5	15.9
			Perlidae						
				Eccoptura	5.90	61	<0.0001	0.6	5.7
			Perlodidae						
				Clioperla	6.07	46	<0.0001	1.4	5.5
				Isoperla	6.27	135	<0.0001	0.7	14.6
			Taeniopterygidae						
				Strophopteryx	6.42	39	<0.0001	2.9	9.7
				Taeniopteryx	6.37	27	<0.0001	15.9	20.2
		Trichoptera							
			Hydropsychidae						
				Cheumatopsyche	6.31	277	0.2111	-	35.1
				Diplectrona	5.86	93	<0.0001	1.5	11.4
				Hydropsyche	6.47	160	0.6081	-	43.1
			Leptoceridae						
				Oecetis	5.70	25	<0.0001	0.6	14.5

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Triaenodes	5.17	39	0.1385	-	34.8
			Limnephilidae						
				Ironoquia	4.93	110	0.0232	1.0	16.7
				Pycnopsyche	5.60	103	<0.0001	1.2	5.3
			Philopotamidae						
				Chimarra	6.60	29	<0.0001	0.4	13.7
			Phryganeidae						
				Ptilostomis	5.32	51	0.2463	-	30.6
			Polycentropodidae						
				Polycentropus	5.11	77	0.0045	0.6	11.4
			Psychomyiidae						
				Lype	6.00	82	0.0043	0.7	10.4
			Uenoidae						
				Neophylax	6.26	100	0.0145	1.1	20.5
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				Crangonyx	4.82	233	0.1246	-	35.1
			Gammaridae						
				Gammarus	6.28	200	0.0175	1.1	16.4
				*Stygonectes**	4.92	25	<0.0001	-	41.0
			Hyalellidae						
				Hyalella	5.93	43	0.4047	-	34.8
		Isopoda							
			Asellidae						
				Caecidotea	4.86	376	0.0087	1.2	14.6
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae*		5.36	240	0.0153	-	54.3
		Tubificida							
			Enchytraeidae*		5.46	98	0.0011	-	43.1
			Naididae		6.00	150	0.8399	-	43.1
			Tubificidae						
				*Limnodrilus**	5.79	70	<0.0001	-	43.1
	Plecypoda								
		Veneroida							
			Sphaeriidae						
				Pisidium	5.74	88	0.0916	-	42.3
				Sphaerium	5.95	66	0.0290	0.5	17.2
	Turbellaria								
		Tricladida							

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Planariidae						
				*Dugesia**	6.24	42	0.0016	-	38.0
Piedmont	Enopla								
		Hoplonemertea							
			Tetrastemmatidae						
				*Prostoma**	6.14	29	0.0088	-	29.0
	Gastropoda								
		Basommatophora							
			Physidae						
				*Physella**	6.24	63	0.0331	-	37.3
	Insecta								
		Coleoptera							
			Elmidae						
				Dubiraphia	5.93	50	0.0485	1.6	13.2
				Macronychus	6.50	33	0.0476	2.4	15.7
				Optioservus	6.48	329	0.0036	1.7	11.3
				Oulimnius	6.16	196	0.0140	1.7	12.1
				Stenelmis	6.28	207	0.7957	-	37.8
			Psephenidae						
				Psephenus	6.49	69	0.0046	1.9	14.9
			Ptilodactylidae						
				Anchytarsus	5.93	89	<0.0001	1.3	6.2
		Diptera							
			Ceratopogonidae						
				Ceratopogon	5.60	28	0.4418	-	18.3
				Probezzia	5.90	52	0.0455	0.5	8.8
			Chironomidae						
				*Brillia**	6.23	126	0.0158	-	27.8
				*Chaetocladius**	5.40	37	0.0411	-	23.5
				Conchapelopia	5.91	275	0.3191	-	37.3
				Corynoneura	5.34	150	0.0308	2.4	10.0
				*Cricotopus**	6.12	131	<0.0001	-	37.8
				Cricotopus/Orthocl	6.07	391	0.6801	-	37.3
				Cryptochironomus	6.10	31	0.0239	1.5	14.4
				Diamesa	6.69	301	0.6561	-	27.8
				*Dicrotendipes**	5.82	32	<0.0001	-	37.8
				Diplocladius	5.45	29	0.8188	-	31.8
				Eukiefferiella	6.03	280	0.3621	-	37.3
				Heterotrissocladius	4.94	27	0.7111	-	31.8
				Hydrobaenus	5.50	131	0.9797	-	31.8
				*Meropelopia**	5.66	59	0.0339	-	37.8

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Micropsectra	6.00	151	0.0082	1.6	8.8
				Microtendipes	6.12	132	0.0206	1.6	10.7
				Nanocladius	5.69	58	0.7210	-	30.7
				Orthocladius	6.03	357	0.9682	-	37.8
				Parakiefferiella	5.00	33	0.0202	1.2	10.8
				Parametriocnemus	6.10	512	0.0935	-	35.4
				Paraphaenocladius	5.49	45	0.0408	3.9	12.7
				*Paratanytarsus**	6.19	67	0.0048	-	30.7
				Polypedilum	5.68	241	0.6681	-	37.8
				Rheocricotopus	5.79	82	0.1909	-	24.2
				Rheotanytarsus	6.17	183	0.6000	-	26.8
				Stempellinella	6.43	40	<0.0001	1.0	4.0
				Stictochironomus	5.25	27	0.3875	-	25.1
				Symposiocladius	5.85	26	<0.0001	0.9	9.2
				Sympotthastia	6.72	215	0.1290	-	30.2
				Tanytarsus	5.91	176	0.4115	-	37.8
				Thienemanniella	6.15	192	0.0585	-	27.8
				*Thienemannimyia**	5.45	60	0.0006	-	37.3
				Trissopelopia	5.90	109	0.0402	2.1	9.9
				Tvetenia	5.46	182	0.9241	-	35.4
				Zavrelimyia	5.44	96	0.2194	-	35.1
			Empididae						
				Chelifera	6.32	74	0.0596	-	27.8
				Clinocera	6.70	180	0.0455	2.0	13.2
				Hemerodromia	6.32	170	0.1217	-	37.8
			Simulidae						
				Prosimulium	6.00	439	0.0020	1.4	6.0
				Simulium	5.90	217	0.5425	-	30.2
				Stegopterna	5.11	148	0.0158	3.1	9.9
			Tabanidae						
				Chrysops	5.01	31	0.0263	2.3	14.4
			Tipulidae						
				Antocha	6.66	295	0.8648	-	37.3
				Dicranota	5.74	84	0.0040	2.3	9.1
				Hexatoma	5.63	69	<0.0001	0.5	6.5
				Pseudolimnophila	5.64	75	0.0041	0.8	6.2
				Tipula	6.10	233	0.2850	-	37.8
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	149	<0.0001	1.6	4.3
			Baetidae						

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Acerpenna	6.19	65	<0.0001	0.9	4.0
				Baetis	6.58	70	0.0048	2.3	8.4
			Ephemerellidae						
				Drunella	6.86	30	<0.0001	0.6	1.6
				Ephemerella	6.47	436	0.0020	1.1	5.4
				Eurylophella	6.09	209	0.0119	1.6	11.9
				Serratella	6.86	86	<0.0001	0.8	4.3
			Ephemeridae						
				Ephemera	6.91	28	<0.0001	1.0	2.1
			Heptageniidae						
				Epeorus	6.49	102	<0.0001	0.7	3.0
				Stenacron	6.47	42	0.0456	1.1	14.1
				Stenonema	6.35	377	0.0054	1.1	10.0
			Isonychiidae						
				Isonychia	6.98	148	<0.0001	1.0	3.4
			Leptophlebidae						
				Leptophlebia	5.34	32	0.0239	1.0	4.3
				Paraleptophlebia	6.43	124	<0.0001	0.5	3.5
		Megaloptera							
			Corydalidae						
				Corydalus	6.75	30	0.0263	4.2	14.4
				Nigronia	5.63	102	0.0029	2.7	13.2
			Sialidae						
				Sialis	4.91	35	<0.0001	2.2	9.9
		Odonata							
			Calopterygidae						
				*Calopteryx**	6.00	40	<0.0001	-	37.3
		Plecoptera							
			Capniidae						
				Allocapnia	5.93	51	0.0077	1.3	3.8
				Paracapnia	5.85	43	<0.0001	1.9	3.8
			Leuctridae						
				Leuctra	5.03	45	0.0124	1.2	12.3
			Nemouridae						
				Amphinemura	6.07	310	0.0013	1.2	5.9
				Prostoia	6.04	218	0.0025	1.5	4.7
			Perlidae						
				Acroneuria	6.52	77	0.0042	1.0	6.0
				Eccoptura	5.90	42	<0.0001	4.6	9.9
			Perlodidae						
				Isoperla	6.27	41	<0.0001	0.4	1.9

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Taeniopterygidae						
				Oemopteryx	6.19	26	0.0402	0.8	14.9
				Strophopteryx	6.42	90	<0.0001	1.1	3.5
		Trichoptera							
			Glossosomatidae						
				Glossosoma	6.41	42	<0.0001	0.8	9.9
			Hydropsychidae						
				Cheumatopsyche	6.31	478	0.4197	-	37.8
				Diplectrona	5.86	209	0.0527	-	37.3
				Hydropsyche	6.47	428	0.5092	-	37.8
			Limnephilidae						
				Pycnopsyche	5.60	51	0.0083	0.5	3.9
			Philopotamidae						
				Chimarra	6.60	161	0.0037	1.1	10.7
				Dolophilodes	5.77	50	0.0100	2.4	6.8
			Polycentropodidae						
				Polycentropus	5.11	53	<0.0001	0.9	4.6
			Psychomyiidae						
				Lype	6.00	32	0.0263	0.7	4.7
			Rhyacophilidae						
				Rhyacophila	5.83	141	0.0021	1.2	4.4
			Uenoidae						
				Neophylax	6.26	241	0.0024	1.2	7.1
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				*Crangonyx**	4.82	102	<0.0001	-	34.7
			Gammaridae						
				Gammarus	6.28	35	0.1531	-	21.4
		Isopoda							
			Asellidae						
				*Caecidotea**	4.86	38	<0.0001	-	37.3
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae*		5.36	154	<0.0001	-	37.8
		Tubificida							
			Enchytraeidae*		5.46	76	<0.0001	-	31.0
			Naididae		6.00	195	0.1916	-	37.3
	Plecypoda								
		Veneroida							
			Sphaeriidae						

Appendix B. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Sphaerium	5.95	25	0.0455	0.9	11.3
	Turbellaria								
		Tricladida							
			Planariidae						
				Dugesia	6.24	63	0.2665	-	31.3

Appendix C. Catalog of invertebrate taxa responses to catchment agriculture in Maryland. Taxa with an asterisk (*) displayed a significantly positive relationship with agriculture. For taxa neutrally or positively distributed with agriculture, the T_{95} value represents the maximum catchment urbanization where the taxon was collected. pH represents the level below which streams were not included for analysis.

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
Coastal Plain									
	Enopla								
		Hoplonemertea							
			Tetrastemmatidae						
				Prostoma	6.14	62	0.1217	-	96.7
	Gastropoda								
		Basommatophora							
			Lymnaeidae						
				Pseudosuccinea	6.02	38	0.7111	-	95.7
				*Stagnicola**	6.09	26	0.0455	-	96.7
			Physidae						
				Physella	6.24	173	0.1447	-	99.4
			Planorbidae						
				*Menetus**	5.82	54	<0.0001	-	96.5
	Insecta								
		Coleoptera							
			Dryopidae						
				Helichus	6.29	33	0.3009	-	84.5
			Dytiscidae						
				Agabus	4.46	31	0.0727	-	96.5
				Hydroporus	4.86	111	0.1647	-	99.4
			Elmidae						
				Ancyronyx	6.02	64	0.6229	-	92.2
				*Dubiraphia**	5.93	103	0.0263	-	93.0
				*Macronychus**	6.50	41	0.0108	-	92.2
				Optioservus	6.48	63	0.0667	-	88.5
				Oulimnius	6.16	96	0.0043	25.1	74.6
				Stenelmis	6.28	127	0.7664	-	93.3
			Gyrinidae						
				Dineutus	5.97	51	0.3136	-	86.3
			Haliplidae						
				*Peltodytes**	5.30	30	0.0001	-	89.5
			Ptilodactylidae						
				Anchytarsus	5.93	43	0.0586	-	86.4
		Collembola							
			Isotomidae						
				Isotomurus	5.01	45	0.3409	-	96.5
		Diptera							

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Ceratopogonidae						
				Bezzia	5.80	29	0.5050	-	89.2
				Ceratopogon	5.60	42	0.5283	-	89.2
				*Culicoides**	4.94	26	<0.0001	-	99.4
				*Probezzia**	5.90	48	0.0184	-	99.4
			Chironomidae						
				Ablabesmyia	5.30	125	0.1085	-	95.0
				*Apsectrotanypus**	5.17	42	<0.0001	-	96.7
				Brillia	6.23	71	0.0056	30.4	75.9
				*Chaetocladius**	5.40	34	<0.0001	-	96.7
				*Chironomini**	4.55	49	0.0003	-	96.5
				*Chironomus**	4.55	42	0.0263	-	99.4
				*Clinotanypus**	5.30	49	<0.0001-	-	96.7
				Conchapelopia	5.91	256	0.6041	-	96.7
				Corynoneura	5.34	146	0.4643	-	93.4
				Cricotopus	6.12	142	0.5050	-	99.4
				Cricotopus/Orthocla	6.07	308	0.1349	-	92.6
				Cryptochironomus	6.10	55	0.4047	-	93.2
				Diamesa	6.69	28	0.5050	-	70.2
				Dicrotendipes	5.82	84	0.1531	-	93.0
				Diplocladius	5.45	92	0.5255	-	99.4
				Endochironomus	5.36	28	0.0690	-	82.6
				Eukiefferiella	6.03	155	0.0102	12.9	73.1
				Heterotrissocladius	4.94	42	0.7111	-	96.9
				Hydrobaenus	5.50	143	0.1897	-	96.9
				Labrundinia	6.08	31	0.2061	-	93.0
				Limnophyes†	4.76	35	0.2369	-	87.7
				Meropelopia	5.66	79	0.5951	-	99.4
				Micropsectra	6.00	121	0.0515	-	99.4
				Microtendipes	6.12	93	0.2415	-	96.9
				*Nanocladius**	5.69	91	<0.0001	-	95.0
				Natarsia	5.47	26	0.7619	-	99.4
				*Orthocladius**	6.03	237	0.0447	-	96.9
				Parametriocnemus	6.10	310	0.6671	-	99.4
				*Paraphaenocladius**	5.49	60	<0.0001	-	99.4
				*Paratanytarsus**	6.19	108	0.0003	-	96.7
				*Paratendipes**	6.30	31	<0.0001	-	96.5
				*Phaenopsectra**	5.66	91	0.0003	-	96.9
				Polypedilum	5.68	392	0.2508	-	99.4
				Procladius	5.44	52	0.0640	-	96.7
				Pseudorthocladius	4.89	29	0.6081	-	87.8

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Rheocricotopus	5.79	203	0.1306	-	96.7
				Rheotanytarsus	6.17	194	0.6940	-	95.7
				*Stempellinella**	6.43	34	<0.0001	-	93.3
				Stenochironomus	5.92	51	0.5525	-	89.5
				Symposiocladius	5.85	64	0.0659	-	96.7
				Tanytarsus	5.91	219	0.7870	-	96.7
				Thienemanniella	6.15	125	0.7619	-	89.2
				Thienemannimyia	5.45	46	0.3409	-	84.3
				Tribelos	4.37	81	0.2992	-	96.9
				Trissopelopia	5.90	65	0.6196	-	89.7
				Tvetenia	5.46	104	0.6016	-	92.2
				Xylotopus	5.98	28	0.4418	-	80.7
				Zavrelimyia	5.44	183	0.9511	-	99.4
			Empididae						
				Chelifera	6.32	44	0.1256	-	89.7
				Hemerodromia	6.32	121	0.0655	-	93.2
			Simulidae						
				Prosimulium	6.00	245	0.2665	-	95.0
				Simulium	5.90	193	0.9650	-	93.0
				Stegopterna	5.11	271	0.4353	-	96.9
			Tabanidae						
				Chrysops	5.01	66	0.1217	-	90.2
			Tipulidae						
				Dicranota	5.74	38	0.1699	-	84.1
				Hexatoma	5.63	87	0.0773	-	86.1
				Ormosia	5.30	27	0.0518	-	87.7
				Pseudolimnophila	5.64	95	0.4227	-	99.4
				Tipula	6.10	181	0.5178	-	99.4
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	26	0.0808	-	86.3
			Baetidae						
				Acentrella	6.52	26	0.0690	-	81.7
				Acerpenna	6.19	168	0.0939	-	89.2
			Caenidae						
				*Caenis**	5.87	38	0.0004	-	95.7
			Ephemerellidae						
				Ephemerella	6.47	122	0.6949	-	62.9
				Eurylophella	6.09	134	0.0373	-	85.8
			Heptageniidae						
				Stenonema	6.35	195	0.5156	-	95.0

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Leptophlebidae						
				Leptophlebia	5.34	93	0.0918	-	87.8
				Paraleptophlebia	6.43	29	<0.0001	30.2	76.1
		Megaloptera							
			Corydalidae						
				Nigronia	5.63	89	0.2425	-	86.6
			Sialidae						
				*Sialis**	4.91	41	0.0016	-	93.0
		Odonata							
			Aeshnidae						
				Boyeria	5.85	83	0.0504	-	82.6
			Calopterygidae						
				Calopteryx	6.00	159	0.2539	-	96.9
			Coenagrionidae						
				Argia	6.08	46	0.1876	-	95.7
			Cordulegastridae						
				Cordulegaster	5.49	35	<0.0001	22.1	71.4
		Plecoptera							
			Capniidae						
				Allocapnia	5.93	33	<0.0001	40.9	55.3
			Leuctridae						
				Leuctra	5.03	55	0.0095	24.8	48.0
			Nemouridae						
				Amphinemura	6.07	150	<0.0001	18.9	69.4
				Prostoia	6.04	113	0.0665	-	87.8
			Perlidae						
				Eccoptura	5.90	61	<0.0001	28.7	56.2
			Perlodidae						
				Clioperla	6.07	46	0.1143	-	85.3
				Isoperla	6.27	135	0.0533	-	85.8
			Taeniopterygidae						
				Strophopteryx	6.42	39	<0.0001	48.0	62.1
				Taeniopteryx	6.37	27	0.0690	-	80.1
		Trichoptera							
			Hydropsychidae						
				Cheumatopsyche	6.31	277	0.6028	-	96.9
				Diplectrona	5.86	93	0.0041	30.5	72.1
				Hydropsyche	6.47	160	0.1239	-	93.2
			Leptoceridae						
				*Oecetis**	5.70	25	0.0066	-	88.1

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Triaenodes	5.17	39	0.1385	-	89.5
			Limnephilidae						
				Ironoquia	4.93	110	0.5705	-	95.7
				Pycnopsyche	5.60	103	0.0034	31.6	77.6
			Philopotamidae						
				*Chimarra**	6.60	29	0.0035	-	88.5
			Phryganeidae						
				Ptilostomis	5.32	51	0.0596	-	88.5
			Polycentropodidae						
				*Polycentropus**	5.11	77	0.0395	-	92.2
			Psychomyiidae						
				Lype	6.00	82	0.1531	-	89.7
			Uenoidae						
				Neophylax	6.26	100	0.0655	-	88.5
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				Crangonyx	4.82	233	0.0625	-	95.7
			Gammaridae						
				Gammarus	6.28	200	0.5148	-	99.4
				Stygonectes	4.92	25	0.6637	-	99.4
			Hyalellidae						
				Hyalella	5.93	43	0.4047	-	89.5
		Isopoda							
			Asellidae						
				Caecidotea	4.86	376	0.3665	-	99.4
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae		5.36	240	0.2255	-	96.7
		Tubificida							
			Enchytraeidae		5.46	98	0.6870	-	99.4
			Naididae*		6.00	150	0.0489	-	95.0
			Tubificidae						
				Limnodrilus	5.79	70	0.7976	-	99.4
	Plececypoda								
		Veneroida							
			Sphaeriidae						
				Pisidium	5.74	88	0.7111	-	96.7
				Sphaerium	5.95	66	0.2061	-	99.4
	Turbellaria								
		Tricladida							

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Planariidae						
				*Dugesia**	6.24	42	0.0263	-	96.5
Piedmont	Enopla								
		Hoplonemertea							
			Tetrastemmatidae						
				Prostoma	6.14	29	0.5231	-	87.4
	Gastropoda								
		Basommatophora							
			Physidae						
				Physella	6.24	63	0.1531	-	91.8
	Insecta								
		Coleoptera							
			Elmidae						
				*Dubiraphia**	5.93	50	0.0053	-	92.8
				Macronychus	6.50	33	0.7619	-	90.0
				Optioservus	6.48	329	0.7041	-	100.0
				Oulimnius	6.16	196	0.2925	-	89.5
				Stenelmis	6.28	207	0.9484	-	94.3
			Psephenidae						
				Psephenus	6.49	69	0.8814	-	94.3
			Ptilodactylidae						
				Anchytarsus	5.93	89	0.5255	-	98.1
		Diptera							
			Ceratopogonidae						
				*Ceratopogon**	5.60	28	0.0021	-	100.0
				Probezzia	5.90	52	1.0000	-	100.0
			Chironomidae						
				Brillia	6.23	126	0.8631	-	93.1
				*Chaetocladius**	5.40	37	0.0018	-	93.2
				Conchapelopia	5.91	275	0.1113	-	100.0
				Corynoneura	5.34	150	0.7728	-	100.0
				Cricotopus	6.12	131	0.6392	-	98.0
				Cricotopus/Orthocla	6.07	391	0.8099	-	99.7
				*Cryptochironomus**	6.10	31	0.0018	-	93.6
				Diamesa	6.69	301	0.6048	-	99.7
				Dicrotendipes	5.82	32	0.2113	-	91.4
				Diplocladius	5.45	29	0.3409	-	94.3
				Eukiefferiella	6.03	280	0.4767	-	94.5
				Heterotrissocladius	4.94	27	0.1085	-	99.7
				Hydrobaenus	5.50	131	0.1944	-	91.9
				Meropelopia	5.66	59	0.1297	-	100.0

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				*Micropsectra**	6.00	151	0.0082	-	99.7
				Microtendipes	6.12	132	0.3210	-	98.1
				Nanocladius	5.69	58	0.7210	-	100.0
				Orthocladius	6.03	357	0.3482	-	98.0
				*Parakiefferiella**	5.00	33	0.0064	-	93.1
				Parametriocnemus	6.10	512	0.5032	-	100.0
				Paraphaenocladius	5.49	45	0.8793	-	93.1
				Paratanytarsus	6.19	67	0.0727	-	94.3
				Polypedilum	5.68	241	0.4979	-	95.4
				Rheocricotopus	5.79	82	0.6636	-	84.0
				Rheotanytarsus	6.17	183	0.3687	-	94.3
				Stempellinella	6.43	40	0.1044	-	84.6
				*Stictochironomus**	5.25	27	0.0045	-	90.7
				Symposiocladius	5.85	26	0.4047	-	87.9
				Sympotthastia	6.72	215	0.3908	-	98.1
				Tanytarsus	5.91	176	0.4615	-	95.4
				Thienemanniella	6.15	192	0.5283	-	100.0
				Thienemannimyia	5.45	60	0.6111	-	86.9
				Trissopelopia	5.90	109	0.2486	-	100.0
				Tvetenia	5.46	182	0.6339	-	98.1
				Zavrelimyia	5.44	96	0.2194	-	95.4
			Empididae						
				Chelifera	6.32	74	0.3587	-	95.4
				Clinocera	6.70	180	0.2157	-	88.7
				Hemerodromia	6.32	170	0.3409	-	95.4
			Simulidae						
				Prosimulium	6.00	439	0.5213	-	99.7
				Simulium	5.90	217	0.6081	-	98.0
				Stegopterna	5.11	148	0.0847	-	98.8
			Tabanidae						
				Chrysops	5.01	31	0.2665	-	95.6
			Tipulidae						
				Antocha	6.66	295	0.6791	-	95.4
				Dicranota	5.74	84	0.8910	-	86.9
				Hexatoma	5.63	69	0.0608	-	100.0
				*Pseudolimnophila**	5.64	75	<0.0001	-	99.7
				Tipula	6.10	233	0.1088	-	100.0
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	149	0.0530	-	90.3
			Baetidae						

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Acerpenna	6.19	65	0.4418	-	95.4
				Baetis	6.58	70	0.7976	-	100.0
			Ephemerellidae						
				Drunella	6.86	30	0.0290	69.5	78.4
				Ephemerella	6.47	436	0.2321	-	100.0
				Eurylophella	6.09	209	0.5785	-	95.6
				Serratella	6.86	86	0.7041	-	92.8
			Ephemeridae						
				*Ephemera**	6.91	28	0.0088	-	87.6
			Heptageniidae						
				Epeorus	6.49	102	0.1187	-	94.6
				Stenacron	6.47	42	0.4047	-	87.9
				Stenonema	6.35	377	0.4502	-	100.0
			Isonychiidae						
				Isonychia	6.98	148	0.2279	-	84.0
			Leptophlebidae						
				Leptophlebia	5.34	32	0.3332	-	88.0
				Paraleptophlebia	6.43	124	0.1649	-	98.1
		Megaloptera							
			Corydalidae						
				Corydalus	6.75	30	0.0763	-	83.9
				Nigronia	5.63	102	0.0575	-	87.6
			Sialidae						
				*Sialis**	4.91	35	<0.0001	-	95.6
		Odonata							
			Calopterygidae						
				Calopteryx	6.00	40	1.0000	-	94.6
		Plecoptera							
			Capniidae						
				*Allocapnia**	5.93	51	0.0455	-	95.5
				*Paracapnia**	5.85	43	0.1531	-	90.3
			Leuctridae						
				Leuctra	5.03	45	0.0956	-	94.6
			Nemouridae						
				Amphinemura	6.07	310	0.3328	-	100.0
				Prostoia	6.04	218	0.2576	-	94.6
			Perlidae						
				Acroneuria	6.52	77	0.1456	-	84.0
				Eccoptura	5.90	42	0.1256	-	93.0
			Perlodidae						
				Isoperla	6.27	41	0.3471	-	95.4

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Taeniopterygidae						
				Oemopteryx	6.19	26	0.0502	-	84.6
				Strophopteryx	6.42	90	0.0746	-	95.6
		Trichoptera							
			Glossosomatidae						
				Glossosoma	6.41	42	0.1032	-	83.6
			Hydropsychidae						
				Cheumatopsyche	6.31	478	0.3804	-	94.6
				Diplectrona	5.86	209	0.7140	-	100.0
				Hydropsyche	6.47	428	0.7506	-	95.6
			Limnephilidae						
				*Pycnopsyche**	5.60	51	0.5785	-	98.1
			Philopotamidae						
				Chimarra	6.60	161	0.3471	-	95.6
				Dolophilodes	5.77	50	0.0600	-	85.0
			Polycentropodidae						
				Polycentropus	5.11	53	0.8999	-	83.2
			Psychomyiidae						
				*Lype**	6.00	32	0.0263	-	86.5
			Rhyacophilidae						
				Rhyacophila	5.83	141	0.8189	-	100.0
			Uenoidae						
				Neophylax	6.26	241	0.4026	-	95.6
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				Crangonyx	4.82	102	0.0555	-	94.3
			Gammaridae						
				Gammarus	6.28	35	0.6339	-	98.0
		Isopoda							
			Asellidae						
				Caecidotea	4.86	38	0.1531	-	93.1
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae		5.36	154	0.6034	-	100.0
		Tubificida							
			Enchytraeidae		5.46	76	0.2541	-	94.3
			Naididae		6.00	195	0.6801	-	98.1
	Plececypoda								
		Veneroida							
			Sphaeriidae						

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				*Sphaerium**	5.95	25	<0.0001	-	93.2
	Turbellaria								
		Tricladida							
			Planariidae						
				Dugesia	6.24	63	0.0956	-	99.7
Highlands									
	Gastropoda								
		Basommatophora							
			Physidae						
				*Physella**	6.24	26	<0.0001	-	84.8
	Insecta								
		Coleoptera							
			Elmidae						
				Dubiraphia	5.93	32	0.2113	-	79.8
				Optioservus	6.48	132	0.0503	-	91.1
				Oulimnius	6.16	120	0.0026	6.9	39.1
				*Stenelmis**	6.28	68	<0.0001	-	91.1
			Psephenidae						
				Psephenus	6.49	43	0.0505	-	91.1
		Diptera							
			Ceratopogonidae						
				*Ceratopogon**	5.60	40	0.0173	-	88.2
				Probezzia	5.90	52	0.7719	-	81.7
			Chironomidae						
				Brillia	6.23	44	0.3712	-	82.5
				Conchapelopia	5.91	104	0.5785	-	91.1
				*Corynoneura**	5.34	79	0.0017	-	91.1
				Cricotopus	6.12	26	<0.0001	-	82.7
				Cricotopus/Orthocla	6.07	88	0.5255	-	90.5
				Diamesa	6.69	131	0.4471	-	91.1
				Eukiefferiella	6.03	208	0.6376	-	88.2
				Heterotrissocladius	4.94	38	0.6339	-	76.9
				Micropsectra	6.00	210	0.1836	-	90.5
				Microtendipes	6.12	77	0.3409	-	86.8
				*Orthocladius**	6.03	116	0.0020	-	91.1
				Parachaetocladius	4.97	26	<0.0001	6.3	24.9
				Parametriocnemus	6.10	380	0.8703	-	91.1
				*Paraphaenocladius**	5.49	34	<0.0001	-	91.1
				Polypedilum	5.68	128	0.8739	-	91.1
				Rheocricotopus	5.79	51	0.2279	-	91.1
				Rheotanytarsus	6.17	48	0.2279	-	73.8

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
				Tanytarsus	5.91	104	0.3289	-	91.1
				*Thienemanniella**	6.15	82	0.0002	-	91.1
				Thienemannimyia	5.45	35	0.0608	-	88.2
				Tvetenia	5.46	111	0.8099	-	91.1
				Zavrelimyia	5.44	37	0.7111	-	91.1
			Empididae						
				Clinocera	6.70	31	0.0931	-	73.3
				Hemerodromia	6.32	38	0.1531	-	68.6
			Tipulidae						
				Antocha	6.66	79	0.6339	-	86.8
				Dicranota	5.74	116	0.0078	23.1	68.4
				Hexatoma	5.63	149	0.0810	-	91.1
				*Pseudolimnophila**	5.64	57	0.0339	-	91.1
				Tipula	6.10	104	0.1824	-	91.1
		Ephemeroptera							
			Ameletidae						
				Ameletus	6.31	165	0.0083	6.2	38.8
			Baetidae						
				Acentrella	6.52	32	0.0321	11.7	39.1
				Acerpenna	6.19	42	1.0000	-	86.8
				Baetis	6.58	112	0.6196	-	85.7
			Ephemerellidae						
				Drunella	6.86	35	<0.0001	5.9	31.0
				Ephemerella	6.47	340	0.0344	21.8	53.6
				Eurylophella	6.09	76	0.0568	-	88.2
				Serratella	6.86	40	0.0150	14.6	50.2
			Heptageniidae						
				Cynigmula	6.52	81	<0.0001	8.6	35.4
				Epeorus	6.49	214	<0.0001	6.8	37.0
				Stenonema	6.35	166	0.0235	22.0	50.9
			Isonychiidae						
				Isonychia	6.98	48	0.4828	-	79.8
			Leptophlebidae						
				Paraleptophlebia	6.43	193	0.0518	-	91.1
		Megaloptera							
			Corydalidae						
				Nigronia	5.63	76	0.0047	22.5	42.7
		Plecoptera							
			Capniidae						
				Allocapnia	5.93	31	0.8188	-	87.7
				Paracapnia	5.85	30	0.7111	-	68.4

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Leuctridae						
				Leuctra	5.03	229	<0.0001	15.0	40.0
			Nemouridae						
				Amphinemura	6.07	347	0.0508	-	88.2
				Ostrocerca	4.87	54	<0.0001	6.4	30.9
				Prostoia	6.04	52	1.0000	-	87.7
			Peltoperlidae						
				Tallaperla	4.97	48	<0.0001	15.4	34.7
			Perlidae						
				Acroneuria	6.52	108	0.0028	10.3	68.2
			Perlodidae						
				Clioperla	6.07	32	0.3332	-	87.7
				Isoperla	6.27	132	0.0147	15.3	47.1
			Pteronarcyidae						
				Pteronarcys	6.55	80	<0.0001	9.0	25.6
			Taeniopterygidae						
				Oemopteryx	6.19	49	<0.0001	8.5	21.1
		Trichoptera							
			Hydropsychidae						
				Cheumatopsyche	6.31	186	0.4864	-	88.2
				Diplectrona	5.86	198	0.0107	14.2	47.1
				Hydropsyche	6.47	187	0.7786	-	91.1
			Lepidostomatidae						
				Lepidostoma	5.44	64	0.0062	14.4	53.4
			Limnephilidae						
				Pycnopsyche	5.60	41	0.8607	-	82.6
			Philopotamidae						
				Chimarra	6.60	77	0.7492	-	91.1
				Dolophilodes	5.77	69	<0.0001	8.7	25.7
				Wormaldia	5.21	54	<0.0001	8.0	48.0
			Polycentropodidae						
				Polycentropus	5.11	42	0.1531	-	68.6
			Rhyacophilidae						
				Rhyacophila	5.83	204	0.0168	8.7	48.0
			Uenoidae						
				Neophylax	6.26	229	0.4047	-	91.1
	Malacostraca								
		Amphipoda							
			Crangonyctidae						
				*Crangonyx**	4.82	49	<0.0001	-	82.5
			Gammaridae						

Appendix C. (continued)

Province	Class	Order	Family	Genus	pH	n	χ^2 p-value	D_1	T_{95}
			Asellidae						
				Caecidotea	4.86	101	0.2568	-	90.5
	Oligochaeta								
		Lumbriculida							
			Lumbriculidae		5.36	138	0.0673	-	82.7
		Tubificida							
			Enchytraeidae		5.46	61	0.9085	-	87.7
			Naididae		6.00	65	0.4047	-	91.1
	Turbellaria								
		Tricladida							
			Planariidae						
				*Dugesia**	6.24	32	0.0411	-	81.7

Appendix D. Responses of fish to urbanization gradients delineated by physiographic province. The number of times each species was collected (n) and the filtered pH values are provided. If no deviance between observed and expected distributions was evident, the T_{95} value listed represents the highest level of watershed urbanization where the species was collected. Chi-square values with an asterisk (*) denote positive associations with urbanization. Coastal Plain fishes where eastern shore sites were excluded are noted with a cross (†).

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
Coastal Plain									
	Anguillidae								
	Anguilla rostrata	5.87	560	0.649	-	93.1	0.6899	-	93.1
	Aphredoderidae								
	Aphredoderus sayanus	4.99	270	0.0022	2.2	13.8	0.0011	1.2	12.0
	Catostomidae								
	Catostomus commersoni†	6.60	182	0.1167	-	94.1	0.0010*	-	94.1
	Erimyzon oblongus	5.66	344	0.1322	-	88.1	0.0067	0.6	20.8
	Centrarchidae								
	Enneacanthus gloriosus	5.30	158	0.043	2.0	49.3	0.0034	1.8	37.0
	Lepomis auritus	6.28	208	0.0112*	-	94.1	0.0067*	-	94.1
	Lepomis cyanellus	5.80	91	0.4711	-	88.1	<0.0001*	-	88.1
	Lepomis gibbosus	5.87	400	0.8531	-	93.1	0.2374	-	93.1
	Lepomis macrochirus	6.00	392	0.2394	-	91.1	0.0551	-	91.1
	Micropterus salmoides	6.23	185	0.0352	2.5	58.1	0.0048	37.8	46.6
	Cyprinidae								
	Clinostomus funduloides†	6.46	132	0.164	-	88.1	0.0018	13.8	59.8
	Cyprinella analostana	6.00	88	<0.0001*	-	94.5	<0.0001*	-	94.5
	Luxilus cornutus	6.61	36	0.2665	-	88.1	0.0016	33.9	59.3
	Notemigonus crysoleucas	5.63	244	0.891	-	93.1	0.0040	1.1	36.2
	Notropis hudsonius	6.14	36	0.3009	-	89.6	0.1348	-	89.6
	Notropis procne†	6.47	128	0.0011*	-	94.5	0.0007*	-	94.5
	Rhinicthys atratulus†	6.47	260	0.8814	-	94.5	0.1244	-	94.5
	Semotilus atromaculatus	5.68	109	0.4948	-	94.1	<0.0001*	-	94.1
	Semotilus corporalis	6.37	158	<0.0001	3.7	51.5	<0.0001	5.5	48.0
	Esocidae								
	Esox americanus	5.21	284	0.0232	1.8	41.7	0.0072	1.8	16.1
	Esox niger	5.30	164	0.0244	10.3	55.4	0.0471	11.6	55.4
	Fundulidae								
	Fundulus heteroclitus	6.52	38	<0.0001*	-	94.5	<0.0001*	-	94.5
	Ictaluridae								
	Ameiurus natalis	6.16	101	0.3269	-	80.1	0.2985	-	80.1
	Ameiurus nebulosus	5.63	178	0.6257	-	96.7	0.1639	-	96.7
	Noturus insignis	6.17	118	<0.0001	2.5	41.1	<0.0001	11.3	34.8
	Percidae								
	Etheostoma olmstedi	6.18	424	0.1749	-	88.1	0.0929	-	88.1
	Perca flavescens	4.99	64	0.3009	-	75.4	0.4367	-	75.4
	Petromyzontidae								
	Lampetra aepyptera	5.74	281	0.0032	3.1	42.2	0.0012	2.8	22.7
	Petromyzon marinus	6.35	63	0.3633	-	66.6	0.8652	-	66.6
	Poeciliidae								
	Gambusia holbrooki	5.91	58	0.3633	-	91.9	0.0158	7.3	25.2

Appendix D (cont.)

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
	Umbridae								
	Umbra pygmaea	5.20	647	0.0548	-	91.1	0.0049	1.2	23.9
Piedmont									
	Anguillidae								
	Anguilla rostrata	5.87	252	0.4846	-	93.2	0.3116	-	93.2
	Catostomidae								
	Catostomus commersoni	6.6	564	0.3955	-	93.2	0.0887	-	93.2
	Hypentelium nigricans	6.94	214	0.0179	3.7	43.4	0.0030	2.5	37.6
	Centrarchidae								
	Lepomis auritus	6.28	244	0.7619	-	89.8	0.5034	-	89.8
	Lepomis cyanellus	5.80	239	0.731	-	93.0	0.1539	-	93.0
	Lepomis gibbosus	5.87	131	0.2587	-	92.5	0.0151	5.1	48.1
	Lepomis macrochirus	6.00	311	0.0268	11.1	48.6	0.0025	5.5	44.1
	Micropterus dolomieu	6.7	131	0.0746	-	64.2	0.0518	-	64.2
	Micropterus salmoides	6.23	223	0.0041	4.9	43.4	0.0013	4.5	36.7
	Cottidae								
	Cottus caeruleomentum	6.70	166	0.0071	7.7	44.0	0.0011	3.4	29.7
	Cottus girardi	6.67	139	0.0186	12.4	43.4	0.0033	11.5	33.9
	Cyprinidae								
	Campostoma anomalum	6.94	254	0.5159	-	85.4	0.0116	4.7	46.6
	Clinostomus funduloides	6.46	493	0.0999	-	82.2	0.0028	1.8	33.0
	Cyprinella analostana	6.00	100	0.3409	-	81.6	0.0912	-	81.6
	Cyprinella spiloptera	6.7	66	0.0246	8.6	49.6	0.0016	8.5	42.6
	Exoglossum maxillingua	6.92	290	0.0358	7.2	51.1	0.0026	2.1	43.0
	Luxilus cornutus	6.61	267	0.0077	4.6	45.2	0.0012	3.2	20.3
	Nocomis micropogon	6.05	131	<0.0001	2.8	20.4	<0.0001	2.5	15.2
	Notemigonus crysoleucas	5.63	34	0.2369	-	79.0	0.0156	3.3	45.5
	Notropis buccatus	7.14	54	0.1699	-	71.0	0.0430	5.2	60.5
	Notropis hudsonius	6.14	91	0.0496	17.3	48.1	0.0129	3.0	37.6
	Notropis procne	6.47	133	0.5643	-	89.8	0.0663	-	89.8
	Notropis rubellus	6.70	43	<0.0001	4.1	8.5	<0.0001	4.7	7.3
	Rhinichthys atratulus	6.47	761	0.8397	-	98.5	0.8033	-	98.5
	Rhinichthys cataractae	6.89	511	0.7477	-	93.0	0.4540	-	93.0
	Semotilus atromaculatus	5.68	663	0.4039	-	93.0	0.5547	-	93.0
	Semotilus corporalis	6.37	138	0.0044	5.0	48.1	0.0015	2.7	38.4
	Ictaluridae								
	Ameiurus natalis	6.16	132	0.3607	-	66.4	0.0478	18.1	48.1
	Ameiurus nebulosus	5.63	37	0.0161	18.8	48.1	0.0012	18.1	45.5
	Noturus insignis	6.17	184	0.0158	3.3	43.4	0.0016	2.7	22.6
	Percidae								
	Etheostoma blennioides	6.70	81	0.0358	5.2	43.4	0.0033	1.9	29.7
	Etheostoma flabellare	6.92	170	0.0302	8.8	42.6	0.0135	6.0	41.5
	Etheostoma olmstedi	6.18	389	0.0347	7.2	51.3	0.0058	4.7	43.3
	Petromyzontidae								
	Petromyzon marinus	6.35	46	0.01	2.7	45.6	0.0011	3.1	53.8
	Salmonidae								
	Salmo trutta	6.77	125	<0.0001	2.2	28.8	<0.0001	3.2	20.6
	Salvelinus fontinalis	6.00	47	<0.0001	0.9	13.2	<0.0001	1.6	12.1

Appendix E. Responses of fish to impervious surface cover (ISC) gradients delineated by physiographic province. The number of times each species was collected (n) and the filtered pH values are provided. If no deviance between observed and expected distributions was evident, the T_{95} value listed represents the highest level of watershed ISC where the species was collected. Chi-square values with an asterisk (*) denote positive associations with ISC. Coastal Plain fishes where eastern shore sites were excluded are noted with a cross (†).

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
Coastal Plain									
	Anguillidae								
	Anguilla rostrata	5.87	560	0.5119	-	43.11	0.5515	-	43.11
	Aphredoderidae								
	Aphredoderus sayanus	4.99	270	0.0053	0.63	3.58	0.002	0.78	3.30
	Catostomidae								
	Catostomus commersoni†	6.60	182	0.9219	-	43.11	0.2728	-	43.11
	Erimyzon oblongus	5.66	344	0.1068	-	37.98	0.0035	0.31	6.36
	Centrarchidae								
	Enneacanthus gloriosus	5.30	158	0.0302	0.62	16.88	0.0015	0.73	14.10
	Lepomis auritus	6.28	208	0.0112*	-	43.11	0.3427	-	43.11
	Lepomis cyanellus	5.80	91	0.787	-	43.11	<0.0001*	-	43.11
	Lepomis gibbosus	5.87	400	0.7812	-	43.10	0.1474	-	43.10
	Lepomis macrochirus	6.00	392	0.1414	-	43.09	0.0202	1.33	17.44
	Micropterus salmoides	6.23	185	0.0352	1.10	20.45	0.0044	11.03	15.73
	Cyprinidae								
	Clinostomus funduloides†	6.46	132	0.0715	-	32.69	0.0013	4.40	22.56
	Cyprinella analostana	6.00	88	<0.0001*	-	43.11	<0.0001*	-	43.11
	Luxilus cornutus	6.61	36	<0.0001	10.35	31.88	<0.0001	8.48	18.16
	Notemigonus crysoleucas	5.63	244	0.5528	-	43.11	0.0035	0.17	11.63
	Notropis hudsonius	6.14	36	0.3009	-	37.98	0.1348	-	37.98
	Notropis procne†	6.47	128	0.0001*	-	43.11	0.3419	-	43.11
	Rhinicthys atratulus†	6.47	260	0.3977	-	43.11	0.676	-	43.11
	Semotilus atromaculatus	6.58	109	0.9041	-	36.71	0.0598	-	36.71
	Semotilus corporalis	6.37	158	0.0091	1.04	19.59	0.0093	1.87	15.73
	Esocidae								
	Esox americanus	5.21	284	0.0162	0.54	14.17	0.0058	0.78	4.29
	Esox niger	5.30	164	0.0419	14.10	20.23	0.0358	3.58	20.66
	Fundulidae								
	Fundulus heteroclitus	6.52	38	<0.0001*	-	43.11	<0.0001*	-	43.11
	Ictaluridae								
	Ameiurus natalis	6.16	101	0.5564	-	37.98	0.3354	-	37.98
	Ameiurus nebulosus	5.63	178	0.1933	-	54.25	0.0141	1.10	19.26
	Noturus insignis	6.17	118	<0.0001	1.33	13.72	<0.0001	4.29	11.71
	Percidae								
	Etheostoma olmstedi	6.18	424	0.2052	-	43.11	0.1338	-	43.11
	Perca flavescens	4.99	64	0.1076	-	30.59	0.505	-	30.59
	Petromyzontidae								
	Lampetra aepyptera	5.74	281	0.0032	0.88	12.92	0.0012	0.74	6.40
	Petromyzon marinus	6.35	63	0.3633	-	22.67	0.8652	-	22.67
	Poeciliidae								
	Gambusia holbrooki	5.91	58	0.7613	-	37.98	0.0145	1.24	5.48

Appendix E (cont.)

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
	Umbridae								
	Umbra pygmaea	5.20	647	0.0585	-	42.26	0.0021	0.45	5.48
Piedmont									
	Anguillidae								
	Anguilla rostrata	5.87	252	0.3332	-	37.81	0.3483	-	37.81
	Catostomidae								
	Catostomus commersoni	6.60	564	0.5134	-	37.81	0.1065	-	37.81
	Hypentelium nigricans	6.94	214	0.0408	1.59	14.40	0.0031	1.39	7.97
	Centrarchidae								
	Lepomis auritus	6.28	244	0.7619	-	37.34	0.9558	-	37.34
	Lepomis cyanellus	5.80	239	0.9167	-	37.34	0.0871	-	37.34
	Lepomis gibbosus	5.87	131	0.5629	-	35.12	0.4851	-	35.12
	Lepomis macrochirus	6.00	311	0.0722	-	35.12	0.0697	-	35.12
	Micropterus dolomieu	6.70	131	0.1574	-	20.13	0.4274	-	20.13
	Micropterus salmoides	6.23	223	0.0105	1.98	14.86	0.0024	1.58	9.24
	Cottidae								
	Cottus caeruleomentum	6.70	166	0.0132	1.98	15.16	0.0012	1.57	8.77
	Cottus girardi	6.67	139	0.0357	3.70	14.99	0.0152	2.38	9.24
	Cyprinidae								
	Campostoma anomalum	6.94	254	0.5159	-	37.34	0.0196	1.23	15.16
	Clinostomus funduloides	6.46	493	0.1323	-	37.34	0.0034	1.23	10.66
	Cyprinella analostana	6.00	100	0.6832	-	29.00	0.1355	-	29.00
	Cyprinella spiloptera	6.70	66	0.0055	2.08	15.16	0.0009	1.96	14.86
	Exoglossum maxillingua	6.92	290	0.0439	2.96	15.93	0.0136	1.58	11.83
	Luxilus cornutus	6.61	267	0.0113	1.88	14.91	0.0019	1.12	5.98
	Nocomis micropogon	6.05	131	<0.0001	1.06	4.19	<0.0001	1.11	4.24
	Notemigonus crysoleucas	5.63	34	0.3322	-	21.63	0.0021	7.89	15.99
	Notropis buccatus	7.14	54	0.1699	-	37.34	0.0134	0.42	17.82
	Notropis hudsonius	6.14	91	0.0496	2.08	14.86	0.0127	0.77	7.97
	Notropis procne	6.47	133	0.3538	-	31.34	0.876	-	31.34
	Notropis rubellus	6.70	43	<0.0001	1.19	2.05	<0.0001	1.15	1.95
	Rhinichthys atratulus	6.47	761	0.8022	-	37.81	0.5695	-	37.81
	Rhinichthys cataractae	6.89	511	0.9074	-	37.81	0.7139	-	37.81
	Semotilus atromaculatus	6.58	663	0.6061	-	37.81	0.6573	-	37.81
	Semotilus corporalis	6.37	138	0.0092	1.95	12.09	0.002	1.66	8.54
	Ictaluridae								
	Ameiurus natalis	6.16	132	0.1466	-	32.87	0.105	-	32.87
	Ameiurus nebulosus	5.63	37	0.0413	5.74	16.58	0.0025	13.30	15.29
	Noturus insignis	6.17	184	0.0429	1.26	14.91	0.0018	1.03	7.13
	Percidae								
	Etheostoma blennioides	6.70	81	0.0121	1.68	15.16	0.003	0.83	9.72
	Etheostoma flabellare	6.92	170	0.053	-	37.34	0.0496	2.41	9.04
	Etheostoma olmstedi	6.18	389	0.0443	3.43	15.93	0.0111	1.66	11.32
	Petromyzontidae								
	Petromyzon marinus	6.35	46	<0.0001	1.06	13.22	<0.0001	0.80	13.74
	Salmonidae								
	Salmo trutta	6.77	125	<0.0001	1.21	6.65	<0.0001	0.92	5.98
	Salvelinus fontinalis	6.00	47	<0.0001	0.34	1.80	<0.0001	0.35	1.80

Appendix F. Responses of fish to agriculture gradients delineated by physiographic province. The number of times each species was collected (n) and the filtered pH values are provided. If no deviance between observed and expected distributions was evident, the T95 value listed represents the highest level of watershed agriculture where the species was collected. Chi-square values with an asterisk (*) denote positive associations with agriculture. Coastal Plain fishes where eastern shore sites were excluded are noted with a cross (†).

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
Coastal Plain									
	Anguillidae								
	Anguilla rostrata	5.87	560	0.8513	-	96.7	0.8060	-	96.7
	Aphredoderidae								
	Aphredoderus sayanus	4.99	270	0.4601	-	96.9	0.0846	-	96.9
	Catostomidae								
	Catostomus commersoni†	6.60	182	0.9219	-	70.6	0.6187	-	70.6
	Erimyzon oblongus	5.66	344	1.0000	-	96.7	0.4148	-	96.7
	Centrarchidae								
	Acantharchus pomotis	4.36	26	<0.0001	61.7	75.5	<0.0001	9.7	72.0
	Enneacanthus gloriosus	5.30	158	0.0888	-	93.0	0.0040	64.4	72.0
	Enneacanthus obesus	4.40	50	<0.0001	53.7	72.0	<0.0001	57.8	66.7
	Lepomis auritus	6.28	208	0.0690	-	93.3	0.1913	-	93.3
	Lepomis cyanellus	5.8	91	0.2415	-	99.4	0.4167	-	99.4
	Lepomis gibbosus	5.87	400	0.4589	-	96.7	0.5648	-	96.7
	Lepomis gulosus	5.60	35	0.0186	18.5	55.9	0.0017	14.5	40.4
	Lepomis macrochirus	6.00	392	0.6240	-	96.9	<0.0001*	-	96.9
	Micropterus salmoides	6.23	185	0.3365	-	93.2	0.0702	-	93.2
	Cyprinidae								
	Clinostomus funduloides†	6.46	132	0.6413	-	70.6	0.2199	-	70.6
	Cyprinella analostana	6.00	88	0.0746	-	86.4	0.0075	11.3	72.4
	Luxilus cornutus	6.61	36	0.0009*	-	70.2	<0.0001*	-	70.2
	Notemigonus crysoleucas	5.63	244	0.9879	-	93.2	0.5033	-	93.2
	Notropis hudsonius	6.14	36	0.2061	-	87.8	0.0022	11.7	19.4
	Notropis procne†	6.47	128	0.2327	-	62.1	0.9663	-	62.1
	Rhinichthys atratulus†	6.47	260	0.8533	-	80.9	0.4882	-	80.9
	Semotilus atromaculatus	5.68	109	0.1851	-	87.7	0.1441	-	87.7
	Semotilus corporalis	6.37	158	0.1235	-	93.2	0.0031	72.3	78.2
	Esocidae								
	Esox americanus	5.21	284	0.4982	-	93.0	0.0745	-	93.0
	Esox niger	5.30	164	0.4618	-	96.9	0.2029	-	96.9
	Fundulidae								
	Fundulus heteroclitus	6.52	38	0.6949	-	87.8	0.1008	-	87.8
	Ictaluridae								
	Ameiurus natalis	6.16	101	0.0108	53.9	76.8	0.0051	73.1	78.9
	Ameiurus nebulosus	5.63	175	0.1224	-	93.0	<0.0001*	-	93.0
	Noturus gyrinus	5.47	170	0.5158	-	93.3	0.8656	-	93.3
	Noturus insignis	6.17	118	0.0027	61.8	72.3	0.0019	46.0	70.2
	Percidae								
	Etheostoma fusiforme	4.99	35	0.0186	61.9	74.1	0.0051	64.5	72.0
	Etheostoma olmstedi	6.18	424	0.7126	-	95.0	0.6993	-	95.0
	Perca flavescens	4.99	64	0.1076	-	88.9	0.0039	53.6	72.4

Appendix F (cont.)

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
	Petromyzontidae								
	Lampetra aepyptera	5.74	281	0.6839	-	89.7	0.2790	-	89.7
	Petromyzon marinus	6.35	63	<0.0001	17.5	70.1	<0.0001	22.4	66.2
	Poeciliidae								
	Gambusia holbrooki	5.91	58	0.0339*	-	93.2	<0.0001*	-	93.2
	Umbridae								
	Umbra pygmaea	5.2	647	0.7207	-	96.9	0.0390*	-	96.9
Piedmont									
	Anguillidae								
	Anguilla rostrata	5.87	252	0.1878	-	100.0	0.0970	-	100.0
	Catostomidae								
	Catostomus commersoni	6.60	564	0.7938	-	95.6	0.8247	-	95.6
	Hypentelium nigricans	6.94	214	0.1612	-	85.7	0.1201	-	85.7
	Centrarchidae								
	Ambloplites rupestris	6.05	73	0.1198	-	83.3	0.1109	-	83.3
	Lepomis auritus	6.28	244	0.3787	-	92.7	0.5592	-	92.7
	Lepomis cyanellus	5.80	239	0.5204	-	95.5	<0.0001*	-	95.5
	Lepomis gibbosus	5.87	131	0.2587	-	91.4	0.0651	-	91.4
	Lepomis macrochirus	6.00	311	0.8932	-	95.6	0.2744	-	95.6
	Micropterus dolomieu	6.70	131	0.9794	-	84.3	0.4751	-	84.3
	Micropterus salmoides	6.23	223	0.9382	-	95.6	0.1835	-	95.6
	Cottidae								
	Cottus caeruleomentum	6.70	166	0.1585	-	98.1	0.0673	-	98.1
	Cottus girardi	6.67	139	0.0986	-	88.1	0.0172	67.0	80.7
	Cyprinidae								
	Campostoma anomalum	6.94	254	0.9549	-	91.8	0.0252*	-	91.8
	Clinostomus funduloides	6.46	493	0.1441	-	93.1	0.4602	-	93.1
	Cyprinella analostana	6.00	100	0.3409	-	89.9	0.0187	67.5	78.5
	Cyprinella spiloptera	6.70	66	0.2665	-	86.2	0.5962	-	86.2
	Exoglossum maxillingua	6.92	290	0.2170	-	87.4	0.8741	-	87.4
	Luxilus cornutus	6.61	267	0.2861	-	89.9	0.0898	-	89.9
	Nocomis micropogon	6.05	131	0.0766	-	84.0	0.1058	-	84.0
	Notemigonus crysoleucas	5.63	34	0.2369	-	95.5	<0.0001*	-	95.5
	Notropis buccatus	7.14	54	0.2143	-	86.9	<0.0001*	-	86.9
	Notropis hudsonius	6.14	91	0.3031	-	87.9	<0.0001*	-	87.9
	Notropis procne	6.47	133	0.0857	-	87.4	0.0023	27.9	73.8
	Notropis rubellus	6.70	43	0.3409	-	83.2	0.0039	74.0	74.9
	Rhinicthys atratulus	6.47	761	0.7652	-	100.0	0.5654	-	100.0
	Rhinichthys cataractae	6.89	511	0.4639	-	94.5	0.2575	-	94.5
	Semotilus atromaculatus	5.68	663	0.6061	-	100.0	0.7058	-	100.0
	Semotilus corporalis	6.37	138	0.0343	70.8	79.2	0.0178	66.6	76.7
	Ictaluridae								
	Ameiurus natalis	6.16	132	0.0099*	-	94.5	0.0003*	-	94.5
	Ameiurus nebulosus	5.63	37	0.0761	-	88.0	0.9835	-	88.0
	Noturus insignis	6.17	184	0.8395	-	86.3	0.1842	-	86.3
	Percidae								
	Etheostoma blennioides	6.70	81	0.4343	-	89.9	0.0001*	-	89.9

Appendix F (cont.)

				P/A			Abundance		
Province	Species	pH	n	χ^2 p-value	D_1	T_{95}	χ^2 p-value	D_1	T_{95}
	Etheostoma flaballare	6.92	170	0.5119	-	94.5	0.1807	-	94.5
	Etheostoma olmstedi	6.18	389	0.3284	-	92.8	0.2599	-	92.8
	Percina peltata	6.37	36	0.6339	-	81.5	0.0225	65.3	72.9
	Petromyzontidae								
	Petromyzon marinus	6.35	46	0.0600	-	79.9	0.0011	64.9	74.4
	Salmonidae								
	Salmo trutta	6.77	125	0.0984	-	85.8	0.0587	-	85.8
	Salvelinus fontinalis	6.00	47	0.0808	-	100.0	0.1875	-	100.0
Highlands									
	Catostomidae								
	Catostomus commersoni	6.60	234	0.5502	-	86.8	0.8398	-	86.8
	Hypentelium nigricans	6.94	60	0.4047	-	73.3	0.0047	22.0	37.9
	Centrarchidae								
	Ambloplites rupestris	6.05	83	0.1318	-	81.7	0.0838	-	81.7
	Lepomis auritus	6.28	46	0.6494	-	73.3	0.0082	13.7	56.7
	Lepomis cyanellus	5.80	87	0.1715	-	76.2	0.7354	-	76.2
	Lepomis gibbosus	5.87	56	0.0080	27.1	54.1	0.0012	15.1	39.3
	Lepomis macrochirus	6.00	66	0.2922	-	76.4	0.9114	-	76.4
	Micropterus dolomieu	6.70	59	0.3565	-	79.8	0.0189	13.7	37.9
	Micropterus salmoides	6.23	40	0.0081*	-	74.5	0.0005*	-	74.5
	Cottidae								
	Cottus caeruleomentum	6.70	83	<0.0001	9.0	39.1	<0.0001	11.9	35.4
	Cottus girardi	6.67	118	0.0186	13.3	55.8	0.0312	10.2	56.7
	Cyprinidae								
	Campostoma anomalum	6.94	98	0.2889	-	73.3	0.0107*	-	73.3
	Cyprinella spiloptera	6.70	37	0.2061	-	72.4	0.1585	-	72.4
	Luxilus cornutus	6.61	54	0.0041*	-	79.8	0.1044	-	79.8
	Nocomis micropogon	6.05	52	0.7870	-	73.3	0.0024	43.5	55.3
	Rhinichthys atratulus	6.47	383	0.9487	-	91.1	0.7226	-	91.1
	Rhinichthys cataractae	6.89	170	0.6999	-	84.8	0.3531	-	84.8
	Semotilus atromaculatus	5.68	281	0.2703	-	86.8	0.2368	-	86.8
	Semotilus corporalis	6.37	45	0.4047	-	72.4	0.0702	-	72.4
	Ictaluridae								
	Ameiurus natalis	6.16	40	0.0536	-	73.3	0.0664	-	73.3
	Percidae								
	Etheostoma blennioides	6.70	70	0.7619	-	73.8	0.0301	17.4	65.1
	Etheostoma flabellare	6.92	168	0.0612	-	81.7	0.1839	-	81.7
	Salmonidae								
	Oncorhynchus mykiss	6.51	44	0.8739	-	82.5	0.0177	13.3	50.2
	Salmo trutta	6.77	53	0.0083	11.7	42.7	0.0012	9.2	38.5
	Salvelinus fontinalis	6.00	148	<0.0001	9.2	34.8	<0.0001	8.0	22.4

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